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Integrative biomechanics for tree ecology: beyond wood density and strength

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Abstract

Functional ecology has long considered the support function as important, but its biomechanical complexity is only just being elucidated. We show here that it can be described on the basis of four biomechanical traits, two safety traits against winds (SW) and self-buckling (SB), and two motricity traits involved in sustaining an upright position, tropic motion velocity (MV) and posture control (PC). All these traits are integrated at the tree scale, combining tree size and shape together with wood properties. The assumption of trait constancy has been used to derive allometric scaling laws, but it was more recently found that observing their variations among environments and functional groups, or during ontogeny, provides more insights into adaptive syndromes of tree shape and wood properties. However, over-simplified expressions have often been used, possibly concealing key adaptive drivers. An extreme case of over-simplification is the use of wood basic density as a proxy for safety. Actually, since wood density is involved in stiffness, loads and construction costs, the impact of its variations on safety is non-trivial. Moreover, other wood features, especially the microfibril angle (MFA), are also involved. Furthermore, wood is not only stiff and strong, but it also acts as a motor for MV and PC. The relevant wood trait for that is maturation strain asymmetry. Maturation strains vary with cell wall characteristics such as MFA, rather than with wood density. Finally, the need for further studies about the ecological relevance of branching patterns, motricity traits and growth responses to mechanical loads is discussed.

Keywords

Biomechanics, Ecological strategy, Gravitropism, Shape, Size, Trees, Wood

1 **Introduction**

2 The mechanical design of trees as achieved by Nature, in particular, the perennial self-
3 supporting habit of extremely slender stems, is both fascinating and complex ([Rowe and](#)
4 [Speck, 2005](#)), and understanding how tree and wood traits involved in this design are or are
5 not adapted to the environment is a major challenge in functional ecology. Many physical
6 models have been developed in the past to increase our understanding of why tree design
7 works so efficiently ([Niklas, 1992](#); [Moulia and Fournier-Djimbi, 1997](#); [Niklas et al., 2006b](#)).
8 These models are still used to address some questions that exist in plant ecology today such
9 as the maximum height that trees can reach ([Niklas, 2007](#); [Banin et al., 2012](#)), self-thinning
10 rules ([Larjavaara, 2010](#)), biomass partitioning within tree organs ([Taneda and Tateno,](#)
11 [2004](#)), and developmental, phylogenetic and environmental wood variations ([Watt et al.,](#)
12 [2006](#); [Lachenbruch et al., 2011](#); [Zhang et al., 2011](#)). Indeed, in all of these questions, an
13 understanding of how a given design leads to tree mechanical performance first requires an
14 integrative mechanical framework that lays the groundwork for a dedicated mechanical
15 model ([Niklas, 1992](#)). In such a modelling approach, the mechanical design of a tree is
16 specified by wood mechanical properties and morphological characteristics that make it
17 possible to resist forces and control strains, as well as by their interaction with loads from
18 external factors (wind flows and gravity) and internal factors (supported fresh biomass,
19 crown area, lever arms, etc.). Mathematical expressions can then be derived to explicitly
20 link the tree mechanical performance in terms of strains, stresses and safety margins, to
21 the design variables such as tissue properties and tree size and shape. However, this
22 modelling phase is only a very preliminary step towards understanding how tree and wood
23 traits are or are not ecologically adapted to the environment. From this point of view, most
24 ecologists who speak of biomechanics have actually been focusing on design safety
25 associated with survival ([Read and Stokes, 2006](#)). The two most frequently discussed design
26 features are wood mechanical properties ([Chave et al., 2009](#)) and optimal allometries
27 between height and diameter that maintain a given safety margin against mechanical
28 failure (see Niklas (1994) and Moulia and Fournier-Djimbi ([1997](#)) for a review of related
29 studies, and Niklas et al. ([2006a](#)) for a recent case study).

30 Moreover, as developed by Moulia and co-workers ([Moulia et al., 2006](#)), plant
31 biomechanical performance must continually adapt during growth, implying that a
32 developmental plasticity rather than a genetically-fixed design was probably selected in

33 most environments. Generally speaking, phenotypic plasticity and more accurately
34 ontogenetic plasticity (*i.e.* variation in the ontogenetic trajectory induced by environment)
35 are nowadays widely debated by plant ecologists (Sultan 2002, Wright and McConnaughay
36 2002, Herault *et al.* 2012). Biomechanical ontogenetic plasticity has been widely observed,
37 especially on woody climbers (*e.g.* Menard *et al.* 2009, Rowe and Speck 2006). It is based on
38 mechanosensing that triggers specific growth responses to mechanical signals ([Moulia *et*
39 *al.*, 2011](#)). Analysing these responses has led to the identification of two different
40 components of the support function: (i) a skeletal design based on stem thickness and taper
41 together with the strength and stiffness of wood (Niklas, 1992); and (ii) a motricity design
42 involving active movements generated by mechanical auto-stresses. It has been shown that
43 motricity is required to control the posture of the tree ([Moulia *et al.*, 2006](#)) and to explore
44 its aerial environment ([Martone *et al.*, 2010](#)). So far, advances in plant biomechanics
45 dealing with the involvement of motricity in tree habit and its consequences in terms of
46 mechanical design have been poorly studied in ecology. It is still assumed that plants
47 support mechanical stresses but do not actively generate them (see, for example, how tree
48 biomechanics and reaction wood are presented in Turner, [2001](#)). In their review about
49 biomechanics and plant ecology, [Read and Stokes \(2006\)](#) mentioned ontogenetic variations
50 of mechanical traits due to development constraints as well as stem-righting movements,
51 but biomechanical traits have not integrated such sensing or moving processes up until now
52 (see Chave *et al.* ([2009](#)) about wood traits, and King *et al.* ([2006](#); [2009](#)) about tree
53 mechanical performance). By the same token, plant signalling is an active field of research
54 in ecology ([Givnish, 2002](#)), but mechanical signals have been much less considered than
55 chemical signals, for example.

56 In this paper, we propose concepts and methods that make it possible to better integrate,
57 from an ecological point of view, the way trees mechanically explore their aerial
58 environment “without muscle” ([Martone *et al.*, 2010](#)). Since we emphasize developmental
59 biomechanics during growth, we show that safety against wind damages or against self-
60 buckling is a necessary but not a sufficient condition for the adaptive success of tree habits.
61 We propose a new view of biomechanical performance, describing the biomechanical
62 framework for studying “motricity”, *i.e.*, the ability to slowly but actively control the
63 orientation of stems ([Moulia *et al.*, 2006](#)) by monitoring stem lean and curvature ([Bastien *et*
64 *al.*, 2013](#)) and generating bending forces that actively compensate for the effect of
65 increasing self-loads (Almeras and Fournier, [2009](#)). The way this biomechanical framework

66 has been and could be used in tree ecology at species and community levels is reviewed
67 and discussed.

68 Before beginning this review, we would like to justify why we focused uniquely on trees.
69 Obviously, the previous arguments concern not only trees but all land plants as well (see,
70 for example, [Moulija et al., 2006](#)). However, the long-term adaptation of mechanical design
71 is particularly emblematic in tall and long-living trees. Indeed, during their ontogeny, trees
72 always experiment with a wide range of changing mechanical loads: they increase their
73 mass by up to 10^5 or more during their lifetime. Moreover, cambial growth, although it is
74 not a feature specific to trees ([Lens et al., 2012](#)), has specific implications regarding
75 biomechanics. Contrary to herbaceous plants in which living cells have a significant share in
76 mechanical functions, the bulk of the tree body consists of dead cells that are almost
77 unmodified after their death. Only the very thin living cambium enables through the
78 secondary growth the continuous adaptation of stem mechanical design parameters such
79 as flexural stiffness or orientation over the years. Although the biomechanical comparative
80 analysis of different plant forms is a promising domain (see Rowe and Speck, 2005), we
81 have limited our discussion to woody trees. Moreover, we have primarily focused on forest
82 trees and limited development to the biomechanical performance of aerial support systems
83 mainly focusing on trunks. It is suggested that the reader consults Tobin *et al.* ([2007](#)),
84 Stokes ([2000](#)) and Ennos ([2000](#)) for some insights into root biomechanics. In this review,
85 trees are defined as self-supporting plants where cambial indeterminate growth enables a
86 large and reactive increase of thickness.

87 This review is organized as follows. After introducing briefly the concepts of functional
88 biomechanical traits, we will develop usual mechanical models of strength and safety, and
89 less usual models of motricity, in order to define integrative traits of biomechanical
90 performance at the tree level that combine load characteristics, stem morphology and
91 wood properties. Figure 1 summarizes the mechanical constraints and processes covered.
92 We will discuss how these integrative traits can be estimated by sets of measured traits
93 (obtained by usual or unusual metrologies). Then we will emphasize the interests and limits
94 of scaling laws that link together measured traits under hypotheses of constant
95 biomechanical performance. A specific section will deal with this question of scaling laws
96 along ontogenetic trajectories. Subsequently, we will put stress on wood properties in
97 order to disentangle the different meanings of wood density, a soft trait widely used in
98 ecology, and provide biomechanical interpretations of how wood structure at different

99 level (from tissue to cell wall) could be evolutionarily or physiologically driven. The
100 conclusion will return to general issues, suggesting future research challenges.

101 Symbols are not systematically defined in the text, but can be found in the list of
102 abbreviations at the end. For a better understanding of formulas, readers unfamiliar with
103 biomechanical terms are invited to report to this glossary. General definitions of stresses,
104 strains or auto-stresses are not restated, readers are referred to general reviews (Niklas
105 1992, or Boudaoud 2010), to the general glossary of Moullia (2013), or to definitions (Box 1)
106 of Baskin and Jensen (2013).

107

108 ***Functional biomechanical traits at the tree level***

109 Ecological strategies specify the different ways in which organisms and species secure
110 carbon profit during vegetative growth and ensure gene transmission in the environment
111 where they grow in order to maintain their fitness ([Westoby et al., 2002](#)). To characterise
112 the different strategies, plant ecologists measure functional traits, i.e., “any morphological,
113 physiological or phenological feature measurable at the individual level, from the cell to the
114 whole-organism level, and that impacts fitness indirectly, without explicit reference to
115 environment” ([Violle et al., 2007](#)). Strategies are inferred from the analysis of the
116 relationships between these traits. A major challenge for plant ecology is then: (i) to define
117 consistent sets of measurable traits; and (ii) to develop extensive databases from the
118 recording of these sets of traits in order to quantify ecological strategies of species along
119 environmental gradients ([Violle et al., 2007](#)). These databases are then analysed through
120 multidimensional analysis, revealing syndromes of traits that separate different functional
121 strategies, i.e., clustering of plants among the huge diversity of species and traits, and
122 among the wide range of environments. By doing so, plant ecologists have found only a few
123 basic contrasted strategies ([Westoby et al., 2002](#); [Grime, 2001](#)). Interest has focused on
124 tropical forests since they provide a tremendous diversity of tree species to study
125 strategies. Although a greater number of tree strategies have been discussed for a long
126 time ([Turner, 2001](#); Delcamp et al., 2008; [Fortunel et al., 2012](#)), tropical species have often
127 been opposed along one single predominant axis that expresses growth vs. survival. This
128 axis can be equally interpreted as opposing shade-avoidant or pioneer species vs. shade-
129 tolerant species or dryads ([Turner, 2001](#)). Generally speaking, the question is how traits
130 associated with particular functions such as carbon storage, sap ascent, etc., or mechanical

131 support, are more or less closely linked to this axis. As pointed out by Wright *et al.* (2004), a
132 further question concerns the direct or indirect causality of correlations observed between
133 traits. On the basis of the leaf economics spectrum of Wright *et al.* (2004), Chave *et al.*
134 (2009) reviewed variations of wood properties across large biogeographic gradients and
135 showed that (i) wood basic density ρ is a good proxy for the predominant growth-survival
136 axis, and that (ii) since wood mechanical properties are positively correlated to ρ , a high
137 degree of wood stiffness and strength is also associated with survival. However, the
138 biomechanical causality behind these relationships requires a cautious analysis, bringing us
139 to the issue of mechanical design and the biomechanical modelling of the support function
140 of trees in their environment. Actually, the causality between high wood density and high
141 biomechanical performance is not self-evident and will be widely discussed in further
142 sections.

143 In the following sections, we (i) propose four tree-level integrative traits that characterise
144 the support function and that synthesize the literature on the topic, and (ii) develop a set of
145 biomechanical models that clarifies how wood properties and tree morphology interact
146 with loads to define these integrated traits at the tree level. Indeed, mechanics leads to
147 quite complex geometrical effects compared, for example, to gas exchanges or sap
148 conduction. Whereas the latter are mainly based on fluxes through surfaces, the former
149 involve the transmission of forces through lever arms and second moments of area, leading
150 to geometry-dependent amplifications (Gordon 1978). We show that using integrative
151 models could rebut some intuitive assumptions often made by ecologists such as, for
152 example, “the greater the wood strength is, the greater the safety will be” Indeed,
153 ecologists need to develop a better understanding of integrative biomechanical models that
154 underlie the definition of wood and tree traits: if biomechanical models are designed by
155 physicists alone, there is a risk that they may build only general “first order” models, not
156 adapted to the diversity of life nor to adaptations or responses to specific environments.
157 We show, for example, that shape factors (such as taper or biomass distribution along the
158 stem) have been neglected in the past, despite the fact that their effects on mechanical
159 safety could be important.

160

161 ***Common traits of strength and safety***

162 *Risk of wind damage and tree strength*

163 In trees, wind loading may lead to the most commonly experienced mechanical abiotic risk
164 ([Read and Stokes, 2006](#)). Safety factors against risk are the ratio of the load capability to the
165 actual load ([Niklas, 2000](#)). The higher they are, the higher the margin of safety against the
166 risk will be.

167 Obviously, both wind velocity and air density are environmental factors. In order to define a
168 tree-level trait for wind firmness without any reference to environment, we propose
169 estimating tree safety (SW) as a critical wind drag pressure $\rho_{air} U_w^2$ that makes the trunk
170 break. The usual dimensionless safety factor (Fig. 2 ,[Niklas 2000](#)), can then be obtained as
171 the ratio of our SW trait to the current wind drag pressure, according to specific wind
172 climates. This dimensionless safety factor remains the relevant parameter for discussing the
173 ecological significance of an observed tree design, since the same design could be highly
174 risky in windy conditions and very safe in other ones. Several different mechanistic models
175 have been developed to calculate SW ([Gardiner et al., 2008](#); [Schindler et al., 2012](#)), all
176 based on the following steps: i) estimating the drag force from interactions between wind
177 and crown properties, ii) converting this drag force into bending moments adding the lever
178 arm to any cross-section of the trunk, iii) distributing bending moments in local forces per
179 area unit, namely bending stresses, across the woody cross-section, iv) comparing these
180 stresses due to wind to the maximal stress wood can support, namely wood strength. The
181 stem breaks down if bending stresses exceed wood strength, if not the tree is safe. Then,
182 the critical wind pressure is the one that causes bending stresses just at the limit of wood
183 strength.

184 Quite simple engineering models based on both empirical measurements and physical laws
185 are commonly used by forest managers (see synthesis of [Gardiner et al. \(2008\)](#)) for wind
186 risk assessment. These models overlook the dynamic effects of turbulent flows ([de Langre,](#)
187 [2008](#)) and tree vibrations ([James et al., 2006](#)), including them through a corrective “gust
188 factor” by which the meteorological U_w is multiplied ([Gardiner et al., 2008](#)).

189 Concerning the steps (i) and (ii), wind is assumed to act as a static bending moment
190 calculated at the height X as:

$$191 \quad M_w(X) = 0.5 c_d \rho_{air} A_w U_w^2 (H_w - X) F_w \quad (1)$$

192 This frequently used formulation is more relevant for isolated trees but has also been
193 validated in forestry and included in wind risk management tools ([Gardiner et al., 2008](#)).

194 In such tools, parameters that cannot be directly measured in managed forests are
 195 calibrated. A_w , which is the streamlined projected area of the stem and crown against
 196 which the wind acts, is estimated from basic tree dimensions (H , D , crown dimensions).

197 The shape factor F_w in (1) represents both the interaction between the wind and crown
 198 profiles, and the relationship between the wind around the tree (that is usually not
 199 assessed) and the meteorological data that are available.

200 Then, according to step (iii), the bending moment in (1) is distributed across the cross-
 201 section of the trunk into bending stress $\sigma_w(X)$. Bending stress is locally perceived as forces
 202 per area unit along the trunk axis. The maximum tensile stress is developed on the
 203 windward side whereas maximum compressive stress is located on the opposite leeward
 204 side. Then (step iv), $\sigma_w(X)$ is compared to the wood critical limit for plastic behaviour or for
 205 rupture, $\sigma_c(X)$, measured by bending tests in the laboratory (see general concepts in Niklas
 206 1992 and example of available data in [Chave et al., 2009](#)).

207 To calculate the tree safety, the location X_w of the weakest cross-section (i.e. the height X_w
 208 where damage should occur first) must be estimated. X_w minimises the safety factor
 209 $\sigma_c(X)/\sigma_w(X)$ along the height X . The function $\sigma_c(X)/\sigma_w(X)$ varies along stems with complex
 210 patterns (Niklas, 2000, Fig.2). Actually, a constant stress $\sigma_w(X)$ along the stem is a quite old
 211 and frequently used assumption (e.g. Dean and Long 1986, see Moulia and Fournier-Djimbi,
 212 1997, for a review). Such a constant stress design should constrain the variations of
 213 diameter and wood properties along the stem. However, as claimed by Niklas and Spatz
 214 (2000), such a design agrees neither with empirical observation nor biomechanical theory.

215 Then, as in Niklas (2000), we suggest carefully checking where the minimum safety factor,
 216 $\sigma_c(X)/\sigma_w(X)$ is located. Actually, Figure 2 illustrates a case of complex patterns of variations
 217 of safety with height. Nevertheless, in usual forest trees made of a single and well-
 218 differentiated trunk, safety is usually minimal near the stem base (Gardiner et al., 2008;
 219 Sterck and Bongers, 1998). The critical wind pressure SW is then calculated at the stem
 220 base as:

$$221 \quad SW = \frac{\pi \sigma_c D^3}{16 c_d A_w H k_w F_w}$$

222 SW (Safety against Wind) increases with wood strength σ_c and stem thickness D . It
 223 decreases with the drag coefficient c_d , the wind-exposed surface area A_w , and the height of

224 the centre of pressure Hk_w . In the case of a non-circular cross section, the criterion can be
225 easily modified by adding a cross-section shape factor.

226

227 *Are there theoretical limits to the self-supporting habit?*

228 Self-buckling is the mechanical situation where an erect and slender tree is no longer self-
229 supporting, since supported weights exceed a critical limit and make it bend dramatically.
230 This has been identified as another major mechanical constraint on tree stability (Greenhill
231 1881, [Niklas, 1992](#)). Safety against self-buckling is independent of the actual environment
232 since it relies only on the biomass and stiffness characteristics of the tree, without any
233 external factor except gravity acceleration g , whose variations are negligible. Safety against
234 self-buckling is based on the calculation of critical dimensions that the tree mechanical
235 design cannot exceed. According to our previous definition of safety, self-buckling load
236 capability is thus defined as the maximum height a tree can reach before buckling, when
237 other parameters involved in the self-bending loads are kept constant. Then, safety against
238 buckling is the ratio of this maximum height to the actual one.

239

240 *Models of self-buckling safety, calculated as the ratio of the real dimension to the*
241 *theoretical limit*

242 Such a theoretical concept has led to many different models (see the synthesis in Holbrook
243 and Putz, 1989, and Jaouen *et al.*, 2007), all based on the use of two independent
244 dimensions among the thickness D , the height H or the volume V . The simplest one
245 assumes a cylindrical pole loaded with wood weight alone. More complex ones add a
246 power-law taper (Greenhill, 1881), an additional weight at the top of the pole to take leaves
247 and branches into account (King and Loucks, 1978), or a distributed mass along the pole
248 (Holbrook and Putz, 1989). The ratio between the real dimension and the theoretical critical
249 one then gives a dimensionless safety factor against self-buckling (SB), which usually
250 exceeds 1 for normally self-supporting trees. Choosing a parsimonious but accurate model
251 for SB calculation requires experimental validations. Whereas Holbrook and Putz ([1989](#)) and
252 Jaouen *et al.* ([2007](#)) showed wide discrepancies between different models and discussed
253 their reliability on the basis of observations of trees at the self-supporting limit, most
254 authors trusted the simplest cylindrical pole formula without any discussion (see Sterck and
255 Bongers, [1998](#); Osunkoya *et al.*, [2007](#) and Read *et al.*, [2011](#), among others). Both Jaouen *et*

256 *al.* (2007) and Holbrook and Putz (1989) showed that in the tree sapling samples they
 257 studied, the simplest cylinder formula fits well with more realistic models that account for
 258 trunk shape and load distribution. Figure 3 illustrates this result since the safety factor of
 259 the crowned stem (iv) is better approximated by the cylinder (ii) than by the tapered stem
 260 (iii). Actually, the additional weight gained by considering a cylinder roughly compensates
 261 for the weight of branches and leaves, disregarded in the tapered stem model. However, in
 262 many works that focused on self-buckling through the cylindrical pole model, crown
 263 morphology was considered as an important tree functional trait (Sterck and Bongers,
 264 1998; Osunkoya *et al.*, 2007). Since results pointed out that branches and leaves should
 265 have different weights from one species to another, it was unfortunate that the crown
 266 morphology could not have been integrated into calculations of self-buckling safety.
 267 Indeed, Jaouen *et al.* (2007) demonstrated that both the stem taper and the height of the
 268 tree centre of mass explain a larger part of the variation of the critical self-buckling height
 269 than, for example, the wood modulus of elasticity. Thus, the soundness of a general
 270 cylinder pole model, which is the least physically relevant, is questionable.

271 More generally, should other additional weights (such as ice, rainfalls or snow, epiphytes,
 272 animals, etc.) be included in the calculation of the critical self-buckling height? Obviously, as
 273 it is generally implicitly assumed since Greenhill (1881), they can be considered as random
 274 events, associated with an oversized design to face uncertainties. That is why a safety factor
 275 SB that is too close to 1 is not viable, whereas an optimal SB would be probably a bit larger
 276 than 1 (King *et al.* 2009). For additional accuracy, an estimation of these additional weights
 277 could be included in critical height calculations (Holbrook and Putz 1989, King and Loucks
 278 1978). When comparing ecological situations of different regimes of rainfalls or of variable
 279 abundance of epiphytes or lianas, such detailed approaches would make it possible to
 280 quantify how much more safety is required in the most constrained environments. Actually,
 281 the height of the centre of mass - m parameter – may have been substantially
 282 underestimated, as well as the load factor, when abusively neglecting epiphytes, ice or
 283 snow. In Fig. 3, models of increasing complexity have been used to calculate SB on a tree of
 284 a given diameter and height, assuming less and less uncertainty concerning loads (practical
 285 formulas are given above, inputs are developed in the legend). Figure 3 demonstrates that
 286 additional weights (case (v)) could have an impact on SB on the same order of magnitude as
 287 taper or crown load.

288 In any case, the magnitude of the safety factor bears important ecological information in
 289 itself: a low safety factor (close to 1) indicates a real risk, whereas a high safety factor

290 instead suggests that the constraint is not ecologically relevant or improperly calculated
291 since important drivers have been neglected. Then, as reported by Niklas and Spatz ([2004](#)),
292 it is really problematic to assume that the tree biomechanical design is driven by a constant
293 and high safety factor. Therefore, each time a high safety factor (higher than 5 to 10, for
294 example) is observed, both the relevancy of the biomechanical constraint (is buckling a real
295 risk?) and the method used for calculation (are loads, shape or wood properties properly
296 assessed?) must be questioned.

297

298 *The critical self-buckling height refers to different dimensional limits, depending on*
299 *environmental drivers*

300 As effectively pointed out by Holbrook and Putz (1989), calculating critical dimensions
301 addresses a last but sensitive question: should we calculate the critical minimum diameter
302 with a fixed height of the tree? Alternately, should the basal diameter be maintained
303 constant to calculate the critical maximum height? This choice must be discussed from an
304 ecological perspective. Buckling is a great limiting mechanical constraint when the intense
305 competition for light foraging is the main environmental force at play, suggesting that
306 investment capability in the support function is limiting. Maximum height for a given
307 support tissue volume (or biomass) would then be meaningful, as assumed by Jaouen *et al.*
308 (2007) and Holbrook and Putz (1989) when dealing with understorey trees, where trees are
309 sheltered from winds but allocate comparatively more biomass to height growth than to
310 diameter increment. On the other hand, when comparing canopy trees of similar height,
311 minimising the diameter or the volume of support tissue for a given height, as done by King
312 *et al.* (2009), is also relevant.

313 Whereas the above-mentioned authors carefully rewrote Greenhill's criterion to argue their
314 choice of critical self-buckling dimensions, most authors use the formula based on a
315 constant diameter without any ecological justification (e.g., Sterck and Bongers, 1998,
316 among others). Maximising height at a forced constant diameter can be the relevant
317 criterion to compare plants from a wide variety of biological types or plants, including
318 species that lack perennial secondary growth (Niklas, 1992). However, among trees
319 characterised by indefinite growth in thickness, using a fixed diameter seems difficult to
320 justify.

321

322 Practical criteria to estimate the safety margin against self-buckling

323 The following section gives practical equations (provided as supplementary material in a
324 .xlsx file) to compute safety against self-buckling, adapted to populations of varying heights
325 based on the maximum height achievable with a constant support tissue volume. By
326 reformulating Greenhill's model ([1881](#)) and revisiting Jaouen's formula (2007), the critical
327 self-buckling height is:

$$328 \quad H_c = 0.88 V^{1/4} E^{1/4} (\rho_T g)^{-1/4} F_b^{1/2}$$

329 The density of the carried load ρ_T is significantly higher than the fresh density of wood
330 alone ρ_{green} , or than the wood basic density ρ , sometimes improperly extended to SB
331 calculations ([Sterck and Bongers, 1998](#)). The shape factor F_b is 1 when the tree is
332 represented by a cylindrical pole loaded by its own mass alone, as recently assumed by
333 most authors. In other situations, it is a function of biomass and diameter profiles along the
334 stem:

$$335 \quad F_b = 0.1785 (|m - 4n + 2|) \cdot (2n + 1) \frac{J_{\frac{4n-1}{m-4n+2}}^{-1}(0)}{J_{\frac{4n-1}{m-4n+2}}^{-1}(0)}$$

336 The parameters n and m are defined by $D(X) = D \left(\frac{H-X}{H} \right)^n$, and $M(X) = \rho_T V \left(\frac{H-X}{H} \right)^m$,
337 where $D(X)$ is the diameter at height X and $M(X)$ is the biomass supported above height X .
338 The higher n is, the higher the taper will be ($n=0$ is a cylinder). The higher the value of m is,
339 the nearer to the base of the tree the biomass is concentrated. $m+1$ is the ratio of the total
340 height to the height of the centre of mass H_g (Fig. 1). The Bessel function first root
341 $J_{\frac{4n-1}{m-4n+2}}^{-1}(0)$ can be practically solved with an adapted computing software programme or by
342 using the linear regressions fitted by Jaouen *et al.* (2007). The safety factor SB is then
343 defined as the ratio H_c/H . Since the volume V is $\pi H D^2 / (4(2n+1))$ ([Jaouen et al., 2007](#)), SB is
344 given by the following equation:

$$345 \quad SB = 0.836 H^{-3/4} D^{1/2} E^{1/4} (\rho_T g)^{-1/4} (2n + 1)^{-1/4} F_b^{1/2}$$

346 Safety against self-buckling increases with wood stiffness E , the amount of support tissue V
347 or the diameter D , and decreases with height H and specific mass ρ_T .

348 It can be observed that for a cylinder ($n=0$, $F_b = 1$), this SB based on constant volume is a
349 power of $\frac{1}{4}$ of the widely used safety factor $0.792 H^{-1} D^{2/3} E^{1/3} (\rho_T g)^{-1/3}$, based on a

constant diameter (which is then higher, as shown in Fig. 3). Actually, the three safety factors calculated from (i) a minimum diameter at constant height, (ii) a maximum height at constant diameter, or (iii) a maximum height at constant volume, are closely related. Due to the multiplicative relationships linking H_c , H , D and V , they are powers of each other. Therefore, they can be used indifferently for comparing safety between trees, regardless of the ecological conditions. Moreover, the limit for the self-supporting habit is always 1, and the optimal allometry between H and D that leads to constant safety during growth (assuming that the other parameters are constant) is also $H \sim D^{2/3}$, regardless of the criterion.

358

359 ***Including motricity in functional biomechanical traits***

360 *Motricity of lignified stems: what enables trunks to actively curve?*

Although trees have been idealised as perfectly vertical structures when calculating SW or SB traits, real trees always lean, at least slightly. Without any gravitropism, trees could not maintain a vertical orientation because their increasing weight would always bend them towards the ground. As highlighted by Darwin and Darwin (1880), gravitropism is a major growth process that takes part in light foraging strategies and is achieved through local curving along stems and auto-stressing systems (Archer and Wilson, 1973; Hejnowicz, 1997). Curving stiff, thick and lignified tree stems requires a specific source of energy, supplied by an internal straining process, leading to asymmetric auto-stresses (Martone et al., 2010). In radially growing stems and differentiating wood, this process, namely the maturation strain induction, occurs at the end of cell formation, and the asymmetry is achieved through the differentiation of reaction wood (Scurfield, 1973). After reviewing traits of the skeletal design, we now formalise which tree features characterise the motricity design.

Following the work of Fournier et al. (1994a), Almeras and Fournier (2009) modelled the bending curvature of a growing stem due to auto-stresses as:

$$\frac{dC_m}{dD}(X) = -4 \frac{F_m(X) \Delta\alpha(X)}{D(X)^2}$$

This minimal model expressed the basic limits and drivers of the movement: tropisms require growth, so the model represents a rate of curvature per unit of radial growth in diameter (dC/dD). The thinner the stem is, the easier the bending will be and, moreover,

the rate of curvature is proportional to D^{-2} . Motricity is then less constrained in thin axes, as noticed by Collet et al. (2011) or Jaouen (2007) studying saplings, and then carefully discussed by Dassot et al. (2012) on beech stands of different tree density or by Almeras et al. (2004) on branches. The difference in maturation strain $\Delta\alpha$ from one side to the other is the main driving force that generates an asymmetry of pre-stresses. Radial growth asymmetry is an additional way to generate such an asymmetry from the mean value $\bar{\alpha}$: stems curve by making more straining wood and/or more wood of the same quality on one side. The shape factor F_m represents the radial growth asymmetry motor as $F_m = 1 + 2k_m \bar{\alpha} / \Delta\alpha$, where k_m is the asymmetry of radial growth, $k_m = (R_+ - R_-) / (R_+ + R_-)$. Actually, Almeras et al. (2005) showed that except in extreme eccentric growth, the second motor is less efficient, so F_m can be taken as 1 in many cases. At a second order, this basic motor process is also catalysed by radial variations of the modulus of elasticity E .

393

394 *Moving as fast as possible: the curvature rate as a first trait of motricity*

Curvature velocity $\frac{dC_m}{dt}(X)$ could therefore be a good candidate for describing stem motricity. As reported by Moulia and Fournier (2009), curvature, which is the relevant variable to describe stem movement, follows complex spatial patterns along the stem. Although these spatial patterns by themselves contain information (Bastien *et al.*, 2013), a first approach, focused on time variations, retained curvature velocity near the base (for example, at breast height, which is the usual height of forest measurements) to describe tree motricity, since the bending of the base is essential to move the whole stem (Dassot *et al.*, 2012).

When the lean has been disturbed, trees have to react as fast as possible to recover an adapted posture to avoid losing competition for height growth and light foraging (Fournier *et al.*, 2006). A first motricity trait is therefore defined as tropic Motion Velocity (MV), i.e., the curvature rate near the base due to radial growth and maturation strains:

$$MV = \frac{dC_m}{dt}(0) = -4 \frac{F_m \Delta\alpha}{D^2} \frac{dD}{dt}$$

MV is the way the trunk is able to react to disturbances of the trunk lean from its set-point angle by generating asymmetric pre-stresses at the stem periphery. The trunk set-point

410 angle is driven by the environment. It is generally vertical, leading to negative
411 orthogravitropism, but becomes oblique on slopes ([Matsuzaki et al., 2006](#); [Lang et al.,](#)
412 [2010](#)), or during regeneration stages in shade conditions ([Collet et al., 2011](#)), due to
413 interactions with phototropism.

414

415 *Competition for light, slenderness and long-term stability*

416 As a founder of biomechanics, Gordon (1978) stated that Nature seems to have accepted
417 stiffness quite reluctantly, except in trees that must be both light and rigid. However the
418 incredibly low stiffness of a slender young sapling tree competing for light would puzzle any
419 civil engineer responsible for design of such a tall, heavy and durable structure exposed to
420 winds and other loads, as a tree should be. Then, since trees are very common elements of
421 our landscapes, a question of more ecological relevance is how such a design can grow and
422 remain upright for such a long time ([Moulia et al., 2006](#)). Actually, wood produced at the
423 tree stem periphery is not only a rigid and strong perennial material, as it is in wood houses
424 built by humans, but the tissue of a smart thickening process as well. This process enables
425 the physiological acclimation of the support system to changing mechanical constraints and
426 increasing supported masses, but requires a tremendous coordination between growth in
427 diameter and height (or biomass), on the one hand, and growth and wood properties,
428 especially maturation strains, on the other. According to Grime's strategies ([Grime, 2001](#)),
429 in environments with low wind stress and disturbance (low chronic winds, no storms, no
430 sudden changes of wind sheltering such as forest understories not disturbed by large gaps),
431 trees should develop a high efficiency to compete for the light resource, at a low cost to
432 support tissue. Since stems become very slender and close to the non-self-supporting habit
433 in such conditions, a first above-mentioned criterion of biomechanical performance is
434 safety against self-buckling. It is a necessary condition but not a sufficient one. As soon as a
435 tree is slightly disturbed from perfect verticality and symmetry, further growth in biomass
436 makes it bend downwards so that motricity must be activated to control a safe posture
437 over time.

438

439 *Maintaining an erect habit: moving to compensate gravitational bending*

440 The biomechanical performance of erect trees is thus based on the way trunks are able to
 441 maintain the trunk set-point angle by the above-mentioned active curving. Almeras and
 442 Fournier (2009) suggested defining such a biomechanical performance as follows:

443 i) Growth in biomass induces a curvature rate due to the continuous change of
 444 biomass in a growing tree (near the stem base, $X=0$). It can be calculated as:

$$445 \quad \frac{dC_g}{dD} = 16(1+b)F_g \sin\varphi \frac{\rho_T g}{E} \frac{H^2}{D^3}$$

446 The higher the load ρ_T , the lever arm H and the lean φ are, and the lower the stem
 447 thickness D and the wood stiffness E are, the higher the flexibility $\frac{dC_g}{dD}$ will be. The form
 448 factor F_g is 1 in a cylindrical pole ($n=0$ and $m=1$), and in other situations, for a given total
 449 biomass (fixed by ρ_T , H and D), the higher the centre of mass is, the higher F_g will be.
 450 Through the allometric exponent b , the bending under self-weight also increases when
 451 relative growth in height compared to relative growth in diameter is more rapid.

452 ii) Therefore, the performance of posture control (also called gravitropic performance
 453 by Almeras and Fournier, 2009) is the ratio of the value of the reaction, i.e., the
 454 tropic motion rate per unit of radial growth $\frac{dC_m}{dD}$, to the gravitational curvature
 455 rate $\frac{dC_g}{dD}$.

$$456 \quad PC = \frac{-dC_m}{dC_g} = \frac{E \Delta\alpha}{4(1+b) \rho_T g \sin\varphi} \frac{F_m D}{F_g H^2}$$

457 Like previous biomechanical integrative traits, PC is the balance between a load action
 458 independent of environmental factors, in this case, $F_g \rho_T g \sin\varphi$, and a tree reaction, in this
 459 case, $F_m E \Delta\alpha$. Size and shape interacts with these latter actions and reactions, with an
 460 immediate effect of size through D and H . $PC=0$ means that the tree is not able to react any
 461 longer. Therefore, it will bend more and more under its self-weight. $PC=1$ is the situation
 462 where a given posture is maintained when no more bending, upward by reaction or
 463 downward by gravity, occurs. When $PC>1$, the tree is righting itself, whereas when $PC<1$, it
 464 is sagging down.

465

466 *Functional diversity and variations of motricity traits*

467 When dealing with the diversity of tree functional traits, ecologists have exclusively
468 considered stem biomechanical properties as a way to understand how the tree design
469 either avoids or tolerates failure risk. Data collected concerning tree morphology and wood
470 properties are therefore analysed from this standpoint. With this in mind, the assumptions
471 tested were the following: (i) Are high wood strength and stiffness associated with a
472 survival strategy against mechanical constraints and, as a result, with high SB and SW (Read
473 *et al.*, 2011); (ii) Is tree design based on low but optimised stem safety SB or SW that
474 maximises survival and minimises the stem construction costs (Kooyman and Westoby,
475 2009; King *et al.*, 2006); (iii) How can the association between wood density and the
476 growth-survival axis be explained (van Gelder *et al.*, 2006) or disturbed (Read *et al.*, 2011)
477 by biomechanical requirements? We argue that such a view is restrictive and that motricity
478 could also be an important component of tree strategy. Surprisingly, although tropisms are
479 widely investigated via their physiology, their ecological significance has received less
480 attention (Iino, 2006). The two previous motricity traits have been designed to quantify
481 these movements with their different components. PC has been specifically designed as an
482 efficiency trait that should be linked to high survival at low construction costs. Using data
483 from Jaouen (2007), Duchateau (2008) and Delcamp *et al.* (2008), Figure 4 illustrates the
484 use of PC among functional groups in tropical tree communities to investigate relationships
485 between the motricity traits and the demographic ones. PC is variable among species and
486 functional groups, and negatively associated with mortality rate. Actually, the functional
487 response groups defined from species demography, independently of any biomechanical
488 considerations (Favrichon, 1994; Delcamp *et al.*, 2008), appear here to be more
489 discriminated by PC than by SB, which is the usual biomechanical trait of ecologists in such
490 conditions.

491 In addition to PC associated with competition, MV is proposed as an adaptive trait to
492 disturbance. Disturbances such as windstorms, avalanches and landslides immediately refer
493 to the previous biomechanical traits of safety against the abiotic mechanical constraints.
494 However, a general biomechanical view of disturbance should include not only mechanical
495 strength but resilience as well. Thus, a better understanding of how plants explore and
496 colonise space and compete over time in a changing environment is required ([Read and](#)
497 [Stokes, 2006](#)). [Hamilton *et al.* \(1985\)](#) described the switching from a shade-tolerant to a
498 sun-adapted design after gap opening, which is a very common situation of forest
499 community dynamics. Although they were not focused on tropisms and biomechanics, they
500 mentioned righting movements as important morphological adaptations to such a

501 disturbance. Actually, in such situations, the question is no longer how to maintain a given
502 angle to offset the increase of weight (this performance is associated to PC), but mainly to
503 make large and fast movements, described by MV. For instance, in their work on natural
504 regeneration of mixed hardwood forests, [Collet et al. \(2011\)](#) used MV to discuss how the
505 immediate radial growth after gap opening, that speeds up MV, contributed to explain the
506 success of pre-existing advanced regeneration. Actually, an immediate allocation of carbon
507 to cambial growth (which increases motricity and stiffness) with delayed primary growth
508 and crown development (which increase weight) is a strong necessity to avoid long-term
509 mechanical instability.

510

511 ***Four integrative traits of tree stem biomechanical performance obtained by***
512 ***combining size, wood and shape traits***

513 Four integrative biomechanical traits, SW, SB, MV and PC, directly interpretable as
514 properties of the organism, were defined in the previous section. They are linked to the
515 performance or safety of the tree support functions in these two components, the skeleton
516 and the motricity design. We will therefore concentrate on how to use them in ecological
517 studies. First, they must be measurable on great numbers of individuals among the tree
518 diversity and along environmental gradients

519 *Measuring integrative biomechanical traits directly at the whole tree level*

520 The direct measurements of SW and SB traits at the tree level are usually cumbersome. SW
521 can be assessed from wind tunnel experiments ([Cao et al., 2012](#)) or by mimicking wind by
522 pulling tests ([Achim et al., 2005](#)). To enable direct estimation of SB, one needs to define SB
523 as the ratio of the critical load weight to the current one as an increase of tree dimensions
524 up to the critical height or diameter is not feasible. Then, SB may be estimated from
525 artificial loading, adding weights to the tree until it buckles ([Tateno, 1991](#)).

526 The tropic motion velocity MV has been directly assessed through curvature
527 measurements, assuming that the observed changes of curvature are mainly due to the
528 active reaction, neglecting bending under self-weight (Collet et al., 2011). However,
529 observed changes of curvatures always superimpose motricity and bending under
530 increasing weights. On the basis of theoretical models, the two processes can be
531 distinguished from each other through additional measurements, as proposed by Almeras

532 *et al.* (2009) and Huang *et al.* (2010) to analyse gravitropic movements in leaning stems,
533 where the bending under self-weight could no longer be ignored.

534

535 *Assessing integrative biomechanical traits from independent measurements of size, shape*
536 *and wood properties as components of load and resistance*

537 Practically speaking, the four biomechanical traits defined are simple products of wood, size
538 and shape traits (adding a crown property, the drag coefficient c_d , in SW) that could be
539 measured independently. Indeed, some of these dissociated traits are already available in
540 extensive/broad databases: height, diameter and growth rate of H and D are measured in
541 permanent forest plots (Pretzsch, 2009); wood properties such as the modulus of elasticity
542 E or the critical stress σ_c are available in technological databases (Chave *et al.*, 2009). The
543 different dissociated traits are of two types: resistance (compared to motricity) traits
544 describe how the tree resists (compared to reacts) to mechanical constraints, whereas load
545 factors (k , c_d , A_w in SW; ρ_T in SB; or ϕ in PC) describe how the external environment, i.e.,
546 gravity or wind, interacts with the tree structure to transmit forces. In a particular
547 environment, trees can in fact increase their performances by adapting resistance or
548 motricity traits, or can limit the constraint by adapting load factors. Table 1 classifies these
549 components according to their meaning in each integrative trait.

550

551 *The particular case of maturation strains*

552 Maturation strain α is not commonly measured in tree ecology. It can be assessed
553 experimentally (i) by measurements of curvature repeated over time, reversing the model
554 to measure $F_m \Delta \alpha$ (Almeras *et al.*, 2009; Sierra-De-Grado *et al.*, 2008; Coutand *et al.*, 2007,
555 in seedlings and greenhouse experiments; Huang *et al.*, 2010, in relation to branches; and
556 Collet *et al.*, 2011, concerning natural forest regeneration), (ii) by indicators of maturation
557 strains at the stem periphery (Almeras *et al.*, 2005), developed by wood technologists and
558 measured by different stress-releasing techniques (Fournier *et al.*, 1994b; Yoshida and
559 Okuyama, 2002), and (iii) by going back in time from spatial mapping of reaction wood
560 occurrence, using calibrated relationships between reaction wood and maturation strain
561 indicators (Dassot *et al.*, 2012). This last method allows retrospective growth analysis using
562 wood as a marker of past events, as is currently done in dendrochronological approaches.

563

564 ***Scaling or not scaling: how trees follow or evade simple rules derived from***
565 ***constant biomechanical performance***

566 One major theoretical interest of integrative traits is the possibility of using them to discuss
567 scaling laws at constant biomechanical performance. The four integrative traits presented
568 above are based on products of dissociated traits, as size parameters – height, diameter,
569 volume, growth rate and wind surface area -, that interact with wood, load, and shape
570 features. Then, a constant performance (i.e. a constant integrative trait) results in
571 allometric laws that link dissociated traits.

572

573 *Allometric laws between H and D as null hypotheses to test the effect of other variables*

574 Implicitly assuming that size parameters are more variable, theoretical works investigated
575 how height H and diameter D should be coordinated to maintain a constant biomechanical
576 performance, if all the other properties were kept constant. Slenderness laws that maintain
577 a constant safety (SB or SW) have been widely discussed (e.g. King and Loucks (1978), Mac
578 Mahon 1973, Dean and Long 1986, see Chapter 3 of [Niklas \(1994\)](#) and Moulia and Fournier-
579 Djimbi ([1997](#)) for a review). Almeras and Fournier (2009) have derived a similar law for the
580 long-term stability, i.e. a constant posture control (PC). The associated allometric
581 relationships are summarized in Table 1. These scaling laws between size variables provide
582 null hypotheses to investigate how other components of shape, load factor or wood
583 properties could vary with size in order to limit or enhance the size constraints on
584 biomechanical performance.

585

586 *Null hypotheses to be rejected*

587 We would then like to emphasize that the use of integrative biomechanical traits to study
588 how trees adapt to specific environments should not be limited to the “automatic checking
589 of predetermined allometric law between H and D ”. Actually, more exciting results occur
590 when such allometries fail. Dean and Long (1986) emphasized that to maintain a constant
591 SW among trees, a constant $\underline{D}^3 H^{-1} A_w^{-1}$, rather than a simple constant D^3/H , is required.

592 More recently, the possibility that wood variations could compensate for the effect of size
 593 variables become a quite active field of research for tree biomechanics (Niklas, [1997](#);
 594 Waghorn and Watt, [2013](#); van Gelder *et al.*, [2006](#)). The reader can also refer to the section
 595 below on ontogenetic changes. Moreover, a constant biomechanical performance agrees
 596 with neither biomechanical nor ecological theories. Indeed, environmental conditions
 597 orient the value of biomechanical performance and, subsequently, its variation as well as its
 598 ecological relevance. For example, SW in an environment sheltered from the wind is
 599 probably very high (except if this safe environment has been recently changed at the time
 600 scale of evolution or tree development so that trees remain adapted or acclimated to a high
 601 risk). Thus, under such condition, SW is likely to be of little interest. On the contrary, in an
 602 environment where wind is the main constraint SW is meaningful and should be carefully
 603 determined. Actually, in such condition, SW should not rely only on H , D and A_w
 604 adaptations, but also on less studied traits such as drag coefficient or wind pressure area
 605 and the crown reconfiguration with increasing wind velocity (see the theoretical work of
 606 Lopez *et al.*, [2011](#); and the comprehensive experimental study of Butler *et al.*, [2012](#)). Then,
 607 a “wind avoidance” strategy based on optimised values of SW should be much more
 608 complex than simple relationships between H , D and A_w . With regard to self-buckling
 609 safety, mature isolated trees are usually very safe, making allometries derived from
 610 optimised SB factors meaningless (Niklas and Spatz, [2004](#)). However, self-buckling is
 611 adjusted at a minimal level in understories where several saplings are no longer self-
 612 supporting (Jaouen *et al.*, [2007](#)).

613

614 *Weak wood can make strong trees*

615 Many previous works assumed that the higher the wood strength σ_c (or stiffness E) is, the
 616 higher the tree biomechanical performance SW (or SB) will be (e.g. Chave *et al.*, 2009;
 617 Swenson and Enquist, [2007](#)). However, since biomechanical performances are related to
 618 combinations of traits, it is very easy to make a strong trunk with weak wood by just
 619 increasing the diameter. Indeed, as developed by Larjavaara and Muller Landau (2010), due
 620 to the scaling of SW (expressed as $\sigma_c D^3$), decreasing the wood strength by 30% could be
 621 easily offset by increasing the diameter by 10% ($\sqrt[3]{1.3}=1.09$). Therefore, to address the
 622 question of how increasing wood mechanical properties changes the biomechanical
 623 performance, we must take account of how other components of the integrative trait,
 624 especially those such as diameter that considerably vary among trees, scale with wood

625 properties. For example, some authors observed a significant increase in E with slenderness
626 H^3/D^2 (Waghorn and Watt, 2013, in *Pinus radiata*). Waghorn and Watt (2013) discussed the
627 way trees regulated E to maintain a viable level of safety SB at high slenderness, probably
628 using mechanoperception of sways. However, they also concluded that slenderness
629 remains the first driver of SB, so that a higher wood performance E is associated with a
630 lower performance SB. Therefore, only if wood properties are independent of other traits,
631 and if other traits do not vary too much, will the tree biomechanical safety increase
632 significantly with wood strength or stiffness.

633

634 *Scaling laws are based on the assumption of constant integrative traits, that involves*
635 *ecology rather than biomechanics*

636 Biomechanical scaling laws proved to be very popular (e.g. McMahon, 1973), although they
637 are based on complex and cumbersome mechanical models which are not easily
638 understandable by biologists. Therefore, ecologists may think that mechanical theories are
639 the convincing basis of scaling laws. Indeed, when analysing the contribution of size, wood
640 or shape to biomechanical performance, the preliminary mechanical analysis provides
641 answers about the way all the parameters involved interact to generate, transmit or resist
642 forces. However, mechanics cannot say which parameters are constant. First, as above-
643 mentioned, the principle of a constant performance is relative to a tree population in a
644 given environment. Secondly, modelling always uses over-simplifications and neglects
645 parameters. When mechanical integrative modelling is used to derive scaling laws,
646 neglected parameters are implicitly kept constant. Ecology studies which load,
647 morphological and wood traits are variable in tree populations, according to
648 environmental, phylogenetic or physiological limits and drivers. Mechanics can provide help
649 to check by integrative modelling and sensitivity analysis whether these variations impact
650 biomechanical performance. Then, to discuss adaptations of tree biomechanical
651 performance to environment, it would be valid to use comprehensive expressions of
652 integrative biomechanical traits, as proposed in Table 1. For example, in addition to how
653 wood strength σ_c , D and H scale with each other, SW addresses the question of how the
654 load parameters – crown area A_w , lever arm $H k_w$ - could also vary with D , H and σ_c .
655 Similarly, on the basis of a more detailed representation of SB, it follows that taper n and
656 biomass distribution m along the stem should also scale with other traits. Indeed, in tropical
657 forests, weak vs. strong wood, cylindrical vs. tapered stem form, poorly vs. highly

658 developed branching, and a single layer of leaves in the highest parts vs. multi-layered
659 crowns, are associated traits that oppose growth to survival (synthesis in [Turner, 2001](#);
660 [Jaouen, 2007](#)). As reported by ([Niklas and Spatz, 2010](#)), the challenge for biologists is to
661 explore the whole complexity of environmental contexts and tree adaptations of shape and
662 wood properties.

663

664 ***That little tree will grow big!***

665 *Are ontogenetic changes of wood properties and shape functionally significant?*

666 In long-lived organisms such as trees, understanding how observed strong ontogenetic
667 changes in demographic rates could be explained by functional traits is a major issue for
668 ecology ([Herault et al., 2011](#)). From a biomechanical point of view, the increase in size is a
669 major constraint during ontogeny. Therefore, now that we have assessed how functional
670 traits vary with size as well as the above-mentioned null hypotheses on optimal allometries
671 between basic size components, we would like to address the following questions: (i) What
672 are the general variations of wood, shape and load during tree development? (ii) Can these
673 variations and relationships be interpreted by their functional biomechanical role?

674 The variations in mechanical safety as forest trees grow are intriguing since some stages of
675 growth are especially critical, particularly sapling stages exposed to self-buckling in dense
676 understories ([Jaouen et al., 2007](#)), and the oldest stages of canopy trees exposed to wind
677 throws ([Turner, 2001](#)). Some authors have attempted to study how safety factors change
678 with size and ontogeny (see Sterck and Bongers, 1998; Osunkoya *et al.*, 2007; van Gelder *et al.*, 2006). They used expressions of SB based on a constant D , underestimating the load
680 factor ρ_T (taken as ρ) and ignoring shape factors, i.e., the taper and the height of the center
681 of mass, although they did observe variations in crown characteristics. Indeed, their results
682 concerning safety must be considered with caution.

683

684 *Could ontogenetic trajectories of wood properties and shape compensate for size effects?*

685 Using the comprehensive expression of integrative traits as a product of separated traits T
686 at power ν_T , the functional significance of simultaneous ontogenetic variations of wood and

687 shape could be analysed using the following general method. For the purpose of clarity, we
688 have illustrated the method by re-analysing some data from Jaouen *et al.* (2007) concerning
689 SB.

690 The population of 23 individuals of *Oxandra asbeckii* (Pulle) R.E. Fries (Annonaceae)
691 measured by Jaouen *et al.* (2007) are assumed to represent an ontogenetic trajectory (i.e.
692 the different sizes are supposed to represent the same individual at different stages of
693 growth). We have fitted an allometric relationship to estimate the relationship between
694 any trait T (i.e., the size V , the modulus of elasticity E , the shape factor F_b and the load
695 factor ρ_T , and the integrative SB; data from Jaouen *et al.*, 2007) and the height H as $T \sim H^{\tau_T}$.
696 Since H is assumed to follow the ontogenetic trajectory, τ_T is the ontogenetic trend of the
697 variation of T . The ontogenetic trend of SB is therefore the sum of the ontogenetic trends τ_T
698 of all the isolated traits T multiplied by their power exponent ν_T . Table 2 gives the results
699 for the particular sample of *Oxandra asbeckii*: (i) safety against self-buckling decreases with
700 height at a power of -0.23; (ii) if we had studied safety only on the basis of the two size
701 factors H and V , as was done by other authors in the past, we would have concluded that
702 safety decreases with a higher power of -0.32; (iii) additional shape and load factors slightly
703 compensate for size, with a power of +0.02 and +0.06, respectively; (iv) no ontogenetic
704 change was found for the modulus of elasticity. In this particular case, size (i.e., the
705 variations of H , and D or V) remains a constraint, not strongly offset by variations in other
706 features. This general method can apply every time that an integrative trait is a product of
707 dissociated traits.

708

709 *The biomechanical significance of wood properties variations*

710 The way wood properties variations can compensate for size effects during growth is
711 undoubtedly a challenging research question. Analysing black locust trees (*Robinia*
712 *pseudoacacia*), Niklas (1997) estimated that ontogenetic variation of wood properties could
713 maintain SB at a constant level when a tree grows in size. Considering the motricity MV trait
714 that scales with D^2 when other parameters are kept constant, Dassot *et al.* (2012)
715 investigated how adjustments of reaction wood formation would compensate for the highly
716 limiting effect of D during growth in beech (*Fagus sylvatica* L.). Due to the higher content of
717 reaction wood in juvenile wood, they found a high level of stabilisation of motricity during
718 the first young stages that is no longer maintained after ten years of growth. Thus, the

relationship between MV and D was no longer a power law, and decreased faster than the expected D^{-2} . This study of Dassot *et al.* (2012) gave a functional meaning to typical, very frequently reported radial patterns of reaction wood (synthesis in Lachenbruch *et al.*, 2011). Generally speaking, wood radial variations (of density or mechanical properties) are studied in-depth for wood quality assessment in the area of forest science. In a recent comprehensive review, Lachenbruch *et al.* (2011) suggested that adaptation to changing mechanical constraints could explain some typical observed patterns. To test these hypotheses, a first modelling approach would be to assess how the basic integrative traits SB, SW or PC vary with wood radial variations according to simultaneous changes of other dissociated traits (size, shape, load) during growth. As already stated above in relation to scaling with size, inadequate attention has been accorded to shape (such as stem taper and distribution of mass along the stem) and load factor (the total mass per unit of trunk volume or the wind force per unit of crown surface). Indeed, they are as ontogenetically plastic as wood properties. Thus, the ontogenetic change of shape, size, wood and load properties cannot be studied separately. Foresters design forest growth models coupled with wood quality models ([Makela et al., 2010](#); [Auclair and Nepveu, 2012](#)). Since some of these tools simulate simultaneous changes of height, diameter, stem profile, crown expansion and wood variations, they could provide valuable support to investigate how biomechanical performance varies with growth.

738

739 ***A general overview of biomechanical wood traits***

The previous section ended with wood variations since they are likely to have an impact on the ontogenetic trends of biomechanical traits. A general aspect of ecological strategies concerns the way the different properties of wood are related to each other, and the impact of these relationships on the whole organism performance.

744

745 *Wood densities? Simple measurements for a set of distinct functions*

Wood basic density is widely used as a key functional trait indicative of the tree life history and biomechanical and physiological strategies (Chave *et al.*, 2009). In contrast with wood engineering studies where properties of wood with partially dried cell walls are considered, cell walls in the living tree are fully saturated. Water bound within hydrophilic cell walls causes swelling and modifies the cell wall mechanical properties ([Siau, 1984](#)). Conversely,

water present in cell lumens, also called free water, does not play any mechanical role except for the special case of parenchyma cells (Niklas, 1988; Chapotin *et al.*, 2006). It is therefore essential to distinguish between fresh wood density (ρ_{green}) representative of the load (ignoring branches and leaves), and basic density (ρ) representative of the wood mechanical properties (Larjavaara and Muller-Landau, 2010). Assuming that cell lumens are fully saturated in a living tree and that the density of cell wall material is 1500 kg m^{-3} (Kellogg and Wangaard, 1969), fresh density in kg m^{-3} can be approximated by:

$$\rho_{green} = 1000 + \frac{\rho}{3} \quad (2)$$

However, the degree of cell lumen saturation may differ between trees or species, making fresh density a less reliable predictor of interspecific variability of mechanical properties. Basic density ρ is therefore the only appropriate parameter to use as an indicator of wood tissue properties (Larjavaara and Muller-Landau, 2012). The modulus of elasticity of green wood can be predicted from ρ (Fournier *et al.* 2006) as:

$$E = 10400 \left(\frac{\rho}{530} \right)^{1.03} \quad (3)$$

Stiff, heavy and costly high-density wood. Does it make trees more or less safe?

Larjavaara and Muller-Landau (2010) demonstrated that “the lower the wood density is, the greater SW will be”. Such a result sounds surprising. In reality, wood basic density is not only an indicator of wood strength but also of stem construction costs (approximated by the dried biomass) per unit of volume. Therefore, with a given biomass, decreasing wood density will increase the stem thickness. The question is then how the biomechanical performance scales to wood density with a constant dry biomass, that involves a trade-off between wood mechanical properties and stem thickness. Assuming a constant dry biomass of the cross-section actually equals to fix ρD^2 . Then, as SW is proportional to $\sigma_c D^3$, if σ_c varies linearly with ρ (as observed by wood scientists and reported by Chave *et al.*, 2009), the safety SW scales as $\rho^{0.5}$ thus increases with decreasing density (Larjavaara and Muller Landau, 2010). The problem becomes increasingly intricate when the biomechanical performance studied is the safety against self-buckling (SB). In fact, wood basic density becomes not only a proxy for mechanical stiffness E and a component of the construction cost ρ_v , but also a large part of the load since ρ_T is the sum of (i) wood basic density, (ii)

stem water content per unit of trunk volume, and (iii) fresh biomass of leaves and branches per unit of trunk volume. On the basis of a study of tropical trees of 8–25 cm in D (at breast height), and carefully assuming relationships between loads (components of ρ_r) and basic density ρ , King *et al.* (2006) inferred that SB varied slightly, in proportion to $\rho^{0.27}$. Actually, our own simulations presented in Fig. 3 found a similar scaling of SB, between $\rho^{0.22}$ to $\rho^{0.26}$. More recently, [Anten and Schieving \(2010\)](#) studied more generally how the cost to make a trunk of given height and mechanical stability varies with wood basic density. They used the two criteria SW and SB and concluded that a higher density would only result in a slight increase in the safety margin.

790

791 *Theoretical wood variations due to wood structure: ρ and MFA as key structural features*

As mentioned above, the stiffness E and strength σ_c of wood tissues are usually assumed to vary quite linearly with wood basic density (Chave *et al.*, 2009; Fournier *et al.*, 2006). This is a general character of honeycomb cellular materials made of elongated cells, when cell wall properties are constant ([Gibson and Ashby, 1997](#)). Since the density of cell wall material does not significantly differ among wood species, wood basic density represents the relative quantity of the cell wall in a given volume of wood made up of cells and lumens. The quantity of the cell wall material naturally affects the wood tissue properties but cannot explain all of the variability because cell wall stiffness and strength are neither constant nor isotropic. Wood anatomical elements primarily responsible for load carrying are generally aligned with the axis of elongation of the plant organ, which makes wood much stiffer along this direction. Moreover, these load-bearing elements (fibres in angiosperms and tracheids in gymnosperms) exhibit a multi-layered composite cell wall. Some 75% to 85% of the total cell wall thickness consists of a so-called S2 layer made up of a soft viscoelastic matrix that envelops stiff cellulose microfibrils. The latter are organised in spirals that form an angle of typically 10–30°, referred to as the microfibril angle (MFA), with the longitudinal fibre/tracheid axis ([Fengel and Wegener, 1984](#)), and are responsible for most of the stiffness of the cell wall. Stiffness of wood tissues may therefore be expressed as a function of basic density, MFA and cell wall stiffness as follows ([Xu and Liu, 2004](#)):

$$\frac{E}{\rho} = \frac{E_{cw}}{\rho_{cw}} \cos^4 MFA$$

811

812 where E is the elastic modulus or stiffness and the index cw stands for the cell wall material.
813 Since ρ_{cw} is constant, the ratio E/ρ varies with the stiffness of the cell wall along the cell
814 axis, which is primarily determined by the MFA and secondarily by the E_{cw} variations
815 ([Salmen and Burgert, 2009](#)).

816 Concerning other wood properties, strength σ_c is similarly linked to the basic density and
817 MFA ([Evans and Ilic, 2001](#); [Lachenbruch et al., 2010](#); [Read et al., 2011](#)), whereas the
818 amount of strain generated during cell maturation α is quite independent of wood density
819 but related to the MFA ([Clair et al., 2011](#)). Recalling that stem motricity relies on the
820 asymmetry $\Delta\alpha$, the asymmetry $\Delta\alpha$ in hardwoods is the result of the differentiation of
821 tension wood on the upper side, whereas in softwoods, compression wood on the lower
822 side causes the asymmetry. Tension wood is more cellulosic with a low MFA, whereas
823 compression wood is more lignified with a high MFA.

824

825 *Adapting stiffness in the 3D space of basic density, MFA and cell wall stiffness*

826 When observed along wide biogeographic gradients, the correlation between basic density
827 ρ and the modulus of elasticity E ([Chave et al., 2009](#)) has a strong physical determinism,
828 usually interpreted as a trade-off between construction cost and wood performance. In
829 fact, along a wide range of variations of wood density, neither the MFA nor the cell wall
830 stiffness E_{cw} can offset the fact that “the more the better”. The MFA is generally
831 considered in wood science to be intrinsically independent of basic density ([Yang and](#)
832 [Evans, 2003](#); [Boiffin, 2008](#); [Donaldson, 2008](#)). Theoretically, a tree can therefore “choose”
833 to vary one or both properties to adapt its tissues for different loading scenarios, using
834 dense tissues with a low MFA to maximise stiffness E and strength σ_c , low-density tissues
835 with a high MFA to enhance the tissue flexibility (low E), and high-density tissues with a
836 high MFA to enhance the energy absorbed before fracture (called toughness) ([Burgert et](#)
837 [al., 2004](#); [Burgert, 2006](#); [Jungnikl et al., 2009](#)).

838 Typical patterns of association between the three determinants of wood stiffness emerge
839 from the motor function: in softwoods, the high MFA and highly lignified cell walls of
840 compression wood are associated with lower E , with a trade-off between stem safety SB
841 and stem motricity MV ([Almeras et al., 2005](#)). Moreover, since the product $E\Delta\alpha$ is involved
842 in postural control, this lower E could weaken the ability of a stem to maintain a given
843 angle. In hardwoods, motricity is associated with a higher E and there is no trade-off but,

844 instead, a positive association between the performances of both skeletal and motricity
845 function.

846

847 *Some co-variations of ρ and MFA among species are ecologically driven*

848 Studies on interspecific variations of the MFA in ecological contexts are rare since the MFA
849 has mainly been investigated in view of understanding variations in mechanical properties
850 of commercial species in terms of growth conditions ([Saren et al., 2004](#); [Medhurst et al.,](#)
851 [2012](#)) and possible wood quality improvement ([Baltunis et al., 2007](#)). In their pioneer
852 studies, Read et al. (2011) and Boiffin (2008) observed the diversity of the MFA, E and ρ
853 among some rainforest species. While Read et al. (2011) aimed at understanding how high
854 winds in New Caledonia constrained wood properties among 15 species of different sizes
855 and habits, Boiffin ([2008](#)) observed 22 species in French Guiana with a very low wind
856 constraint in understorey saplings from different functional groups of species along a light
857 demand gradient. In both samples, E is closely correlated to ρ (Table 3). In contrast to
858 Boiffin's observations, Read and co-workers (2011) reported that this relationship was not
859 related to the usual growth-survival trade-off in their sample. Indeed, relationships
860 between E and ρ have a strong physical determinism, regardless of the reason why species
861 with low and high wood densities coexist. Moreover, as shown in Table 3, whereas
862 $\cos^4(\text{MFA})$ and ρ are independent among Boiffin's species (2008), they are closely linked in
863 Read et al. (2011), suggesting a strong differentiation of species along a stiffness axis in
864 these high wind conditions. The mean value of the cell wall stiffness, estimated as the
865 average of $E/(\rho \cos^4(\text{MFA}))$, is higher in Read et al. (2011) (with a value of 23.9 GPa) than in
866 Boiffin (2008) (with a value of 21.2 GPa), also suggesting a greater stiffness of the cell wall.
867 Read et al. (2011) raised the question as to why such an opposition between stiff and not
868 stiff wood have been filtered in cyclone-prone environments. Indeed, French Guianese
869 species structured along the light demand gradient make it possible to explore wider
870 possibilities of associations between the MFA and ρ . Read et al. (2011) suggested further
871 studies of the ecological significance of the MFA. Actually, since the MFA is a key feature of
872 motricity, the low mean MFA of some angiosperm species (or high ones of some
873 gymnosperms) could indicate a higher occurrence of reaction wood and, therefore, a higher
874 motricity or postural control. We think that including motricity traits in such investigations
875 will bring new insights into the question of trade-offs or associations between ρ and the
876 MFA.

878 *Beyond the skeleton: including maturation asymmetry $\Delta\alpha$ in wood databases*

879 Studies of the evolutionary significance of PC or MV are in their infancy since they require
 880 measurements of $\Delta\alpha$, which are not the usually collected data in ecological studies. $\Delta\alpha$ is
 881 related to reaction wood formation, which has been widely studied in wood anatomy.
 882 Wood anatomy is strongly linked to evolutionary ecology (Carlquist, 2001). Would it be
 883 possible to use wood anatomical traits as a proxy for $\Delta\alpha$? Indeed, using wood anatomy
 884 databases to infer functional traits is becoming a common practice in ecology (Martínez-
 885 Cabrera *et al.*, 2011). However, translating these anatomical observations into $\Delta\alpha$ is an
 886 unsolved problem, since $\Delta\alpha$ is more closely related to cell wall properties like MFA than to
 887 cellular characteristics usually observed in wood taxonomy. Normal anatomical
 888 observations related to reaction wood, for example concerning the occurrence of the G
 889 layer among tree species, are not useful to assess variations in motricity (Clair *et al.*, 2006)
 890 because different cellular traits associated with different patterns of reaction wood have
 891 converged to the same functionality of motricity traits (Scurfield, 1973).

892 Measurements of α through growth strain indicators (GSI) are now a standard method for
 893 wood scientists (see the large database on European Beech in [Jullien *et al.*, 2013](#)). In order
 894 to enhance high throughput and non-destructive assessment with the sampling methods
 895 commonly used in field ecology, these standards should be used to calibrate indirect
 896 methods using the empirical correlation between GSI and the tangential diameter of an
 897 increment core ([Ferrand, 1982](#)), or, in a more reliable way, the relationship between GSI
 898 and MFA (Yang *et al.*, [2006](#)). New tools such as Silviscan have made extensive
 899 measurements of MFA easier (Read *et al.*, 2011), making it possible to interpret their
 900 variations both as wood stiffness and strength variations related to SB and SW, and as $\Delta\alpha$
 901 and PC or MV variations.

902 Once the appropriate metrology has been selected, the conditions in which maturation
 903 strains are characterised (i.e., the sampling methods) when comparing PC or MV among
 904 species along environmental gradients should also be carefully assessed. When $\Delta\alpha$ was
 905 measured as a righting capacity under controlled conditions of lean disturbance, it was
 906 found to be highly genetically determined (see Almeras *et al.*, 2009, or Sierra-De-Grado *et al.*,
 907 [2008](#)). However, in natural conditions, $\Delta\alpha$ has a high phenotypical plasticity (Fournier *et al.*,
 908 1994b) since it rapidly acclimates to lean disturbances.

910 ***Challenges for future research in ecological biomechanics***

911 *Definition and integration of biomechanical crown traits*

912 In the current definition of integrative traits (SW, SB, PC, MV), branching patterns are
913 included only through the load parameters (m , A_w , c_d , ρ_T). However, trees are complex
914 fractal structure ([Plucinski et al., 2008](#)). The question of relevant traits that capture the
915 biomechanical parts of branching patterns must therefore be addressed. Indeed, the
916 branching structure of the crown has been shown to play a significant role in wind failure
917 through resonant and structural damping behaviours ([James et al., 2006](#)). When studying
918 plant adaptation to the environment, ecology deals with a large number of plants and
919 environments, roughly described at the infra-individual level. Standard biomechanical
920 models based on numerical simulations in which each specific situation is described
921 through a large dataset of variables describing one single tree (e.g., Sellier and Fourcaud,
922 [2009](#)) are thus not appropriate. However, alternative biomechanical studies use
923 parsimonious representations to address questions about the impact of branching patterns
924 on mechanical safety ([Plucinski et al., 2008](#); [Rodriguez et al., 2008](#); [Eloy, 2011](#); [Lopez et al.,](#)
925 [2011](#)). In several models, a simple characterization of branching through two parameters
926 has been found to be sufficient: (i) the branching ratio, which is the reduction of diameter
927 through branching, and (ii) the slenderness exponent, which is the relationship between
928 length and diameter in branch segments ([Rodriguez et al., 2008](#); [Eloy, 2011](#); [Lopez et al.,](#)
929 [2011](#)). For example, using these two branching parameters, [Lopez et al. \(2011\)](#) investigated
930 the brittle reconfiguration of the crown, i.e., the way some branches preferentially break
931 under wind flows acting as mechanical "safety fuses". They proposed an elegant model
932 based on the scaling of the fluid-loading with respect to the critical stress (a criterion similar
933 to SW). Similarly, [Eloy \(2011\)](#) demonstrated that Leonardo's rule (i.e., the total cross-
934 section of branches is conserved across branching nodes) can be a mechanical adaptation
935 to winds. In our opinion, although such models seem very simplistic at first glance, they
936 represent a great potential for ecological studies since they are based on very few
937 parameters of load, size and shape, similarly to popular seminal works such as that of
938 Greenhill (1881).

939

940 *Assessing the evolutionary importance of motricity*

941 As already mentioned above, studies of ecological significance of the variability of motricity
942 traits PC or MV require data about $\Delta\alpha$, which are not as common and available as other
943 wood traits. Using measurements of all other traits of PC, Jaouen (2007) demonstrated the
944 importance of $\Delta\alpha$ variations in sapling growth strategy by *reductio ad absurdum* arguments.
945 She simulated the successive curvatures and leans of saplings under the assumption of $\Delta\alpha$
946 $=0$ (and, therefore, PC=0) for different species competing in a tropical rainforest
947 understorey, under the assumption that the lean has been slightly disturbed at an early
948 stage of growth (Fig. 5). With no capacity of reaction, plants should bend more and more
949 since gravitational curvature acts alone. Then, due to their extreme slenderness and quite
950 high centre of mass, trees would achieve high tilt angles that are even not viable in some
951 species (such as Vm in Fig. 5). Moreover, since stiffness and loads strongly differ between
952 species, this theoretical tilt angle would be highly variable between species. Indeed, such
953 leans and lean variations between species are not observed (Fig.5), demonstrating that
954 motricity is active and that motricity traits necessarily differ between species, as already
955 shown in Fig. 4.

956 However, in nature, trees experience successive disturbances, and the way an observed
957 lean is reached at a given time depends on the whole history of growth and disturbances. In
958 such a context, the success of the righting and straightening process relies on how MV can
959 rapidly adapt after the disturbance. As reported by Almeras *et al.* (2002) who studied the
960 bending of apricot tree shoots, and as shown in theoretical simulations of Fig. 5, even a
961 small difference in stem form at oblique stages before disturbance and in growth rates in
962 response to disturbance could lead, through the reciprocal dependencies between form
963 and growth, to a considerable divergence in its later development. In particular, the timing,
964 size and frequencies of the disturbances should be considered using conceptual approaches
965 of the ecology of disturbances (Johnson and Miyanishi, 2007). Formalising these problems
966 in changing environments along growth trajectories could deeply modify our
967 representation of motricity in natural forests, so far focused on reaction wood formation
968 (Dassot *et al.*, 2012). Indeed, features other than the maturation strain asymmetry
969 ($\Delta\alpha$), such as the relative timing of growth in height, thickness and leaf biomass, may be of
970 greater importance (Almeras *et al.*, 2004). When observing buttress morphology in
971 rainforest species, Chapman *et al.* (1998) concluded that most buttresses are opportunistic
972 organs, the efficiency of which lies in their adaptability to respond to development crises
973 such as gap openings. Actually, as buttresses act as mechanical guy ropes (Clair *et al.*,
974 2003), their formation cause an efficient posture control, without any reaction wood. By

975 the same token, modelling MV or PC in thick and rigid stems of lianas or palm trees, which
976 do not grow in thickness from concentric rings, remains an open question.

977 From a practical point of view, all these studies should use extensive measurements of lean
978 using simple methods (Collet *et al.*, 2011), or new digitising techniques such as T-LIDAR,
979 whose uses are expanding in the areas of ecology and forestry ([Dassot et al., 2011](#)).

980

981 *Towards greater communication between sensory mechanobiology and tree ecology*

982 It is now widely accepted that plants are sensitive to environmental signals, and that signal-
983 driven responses explain a large part of the phenotypical plasticity ([Givnish, 2002](#)). Plants
984 are, in particular, extremely sensitive to wind-induced deformations ([Moulia et al., 2011](#)),
985 as well as to leaning (Moulia and Fournier, 2009), and the thigmomorphogenetic and
986 gravitropic responses are likely to be adaptive in many situations ([Jaouen et al., 2010](#)).
987 However, these responses have been widely ignored in tree ecology.

988 This may be due to the fact that thigmomorphogenesis and gravitropism have long been
989 investigated by plant physiologists in particular, leading to very detailed descriptions at the
990 cellular and molecular level. However, the situation has changed over the last decade. Just
991 as for motricity, parsimonious and generic integrative models have been developed for
992 wind mechanosensing (the S3m model of Moulia *et al.*, 2011) and for postural control (the
993 AC model of Bastien *et al.*, 2013), both of which have been validated on a large set of
994 species and plant habits. These models allow for simple but relevant traits to be defined.
995 For example, Bastien *et al.* ([2013](#)) showed that the mechanosensitive control of posture
996 depends on a single dimensionless parameter B , which is the ratio between the
997 gravisensitivity to lean and the proprioceptive sensitivity of curvature. Moreover, this ratio
998 can be accurately estimated by taking photos at two stages after a leaning disturbance.
999 Finally, these approaches have also revealed genetic markers that may be used as traits of
1000 mechanosensitivity ([Chevolot et al., 2011](#); [Moulia et al., 2011](#)). There is still a significant
1001 amount of work to be done before we can define simple sensory mechanobiological
1002 measurements for tree ecology. In particular, a major challenge will be to integrate these
1003 models over much longer periods of time such as the life span of trees or even climatic
1004 changes. Nevertheless, we think that the conditions are now favourable to promote better
1005 and more fruitful communication between sensory mechanobiology and biomechanical
1006 ecology.

1007

1008 **Glossary of abbreviations and symbols: list (alphabetical order) and definition**

1009 A_w : wind surface area that creates an obstruction to wind flow, depending on crown
1010 dimensions (m^2).

1011 b : ratio of relative height growth to relative diameter growth $(dH/H)/(dD/D)$, i.e., exponent
1012 of the relation $H \sim D^b$ (dimensionless).

1013 c_d : drag coefficient (dimensionless).

1014 D : diameter of the cross-section at the stem base (m).

1015 $D(X)$: diameter of the stem cross-section at X-level (m) .

1016 dC_g/dD : rate of gravitational curvature (downward and positive when weight increases) per
1017 unit of radial growth in diameter near the base (m^{-2}).

1018 dC_m/dD or $dC_m/dD(X)$: rate of reaction curvature (upward and negative in the case of
1019 gravitropism) due to maturation per unit of diameter growth, at the stem base or at X-level
1020 (m^{-2}).

1021 dD/dt : radial growth velocity, usually expressed in mm/year; dD/dt is then twice the annual
1022 tree ring width.

1023 dR_+ : tree ring width on one side + (m).

1024 dR_- : tree ring width on the opposite side – (m).

1025 E : modulus of elasticity (also called Young's modulus) ($N\ m^{-2}$).

1026 E_{cw} : modulus of elasticity of cell wall material ($N\ m^{-2}$).

1027 F_b : self-buckling form factor, $F_b = 0.1785 \left(|m - 4n + 2| \right) \cdot (2n + 1) / \frac{1}{4n-1} (0)$
 $m-4n+2$

1028 (dimensionless).

1029 F_g : growing weight form factor, $F_g = \frac{2}{(m+1)(2n+1)}$ (dimensionless).

1030 F_m : interaction between maturation strains and radial growth asymmetry, which enhances
1031 the motricity (dimensionless).

1032 F_w : wind form factor that represents the interaction between crown shape and wind
1033 profiles (dimensionless).

1034 g : gravity acceleration ($N\ kg^{-1}$).

1035 H : total height of the tree (m).

1036 H_c : critical self-buckling height (m).

1037 H_g : height of the centre of mass (m).

1038 H_w : height of the centre of wind drag pressure (m).

1039 I : second moment of area of the cross-section (m^4).

1040 k_m : eccentricity of radial growth, $k = (R_r - R_i)/(R_r + R_i)$ between -1 and 1
1041 (dimensionless).
1042 k_w : ratio H_w/H , smaller than 1 (dimensionless).
1043 m : biomass profile distribution, defined by $M(X) = p_T V \left(\frac{H-X}{H} \right)^m$, dimensionless. m
1044 represents the relative height of the centre of mass as $m+1 = H/H_g$.
1045 $M(X)$: biomass supported above X-level (kg).
1046 MV: tropic Motion Velocity. Capability of a new peripheral wood to induce a curvature from
1047 the maturation of a new peripheral layer of wood during one unit of time. MV is a
1048 curvature rate ($\text{m}^{-1} \text{s}^{-1}$).
1049 $M_w(X)$: bending moment induced by wind at X-level (N m).
1050 n : taper, defined as $D(X) = D \left(\frac{H-X}{H} \right)^n$, dimensionless. Note that n can be estimated easily
1051 from the form factor $\frac{V}{D^2 H}$ of volume equations of forestry as $\frac{\pi}{4(2n+1)} = \frac{V}{D^2 H}$
1052 PC: Posture Control. Ratio of reaction curvature to gravitational curvature (dimensionless).
1053 SB: tree Safety factor against self-Buckling. Ratio of the maximum height the tree can reach
1054 (while remaining self-supporting with other parameters kept constant), to its actual height
1055 (dimensionless).
1056 SW: Safety against Wind. Tree resistance to wind calculated as the critical pressure $\rho_{air} g$
1057 U_w^2 (N m^{-2}).
1058 T : general symbol for a trait T .
1059 U_w : wind velocity (m s^{-1}).
1060 V : volume of the trunk (m^3).
1061 $\Delta\alpha$ or $\Delta\alpha(X)$: contrast of maturation strain in the new ring of wood of a growing stem, at
1062 the stem base or X-level (dimensionless).
1063 φ : mean lean of the stem, angle from the vertical (radian).
1064 ν_T : general power of a dissociated T in the expression of an integrative trait.
1065 ρ : wood basic density, which is the mass of dried wood per unit of fresh volume (kg m^{-3}).
1066 ρ_{air} : density of air in kg m^{-3} . ρ_{air} can be calculated from temperature, air relative humidity
1067 and elevation. For 15°C , 60% of relative humidity, $\rho_{air}=1.21 \text{ kg m}^{-3}$ at sea level.
1068 ρ_{cw} : basic density of the cell wall material, $\rho_{cw}=1500 \text{ kg m}^{-3}$.
1069 ρ_{green} : density of green wood in the living tree, ratio of fresh mass (dry matter and water) to
1070 fresh volume, in (kg m^{-3}).
1071 ρ_T : total fresh biomass supported, including leaves, trunk and branches, per unit of trunk
1072 volume (kg m^{-3}).

1073 σ_w or $\sigma_w(X)$: bending stress induced by wind forces, at the stem base or at X-level (N m^{-2}).
1074 σ_c or $\sigma_c(X)$: wood critical stress usually measured by bending tests (as the standard MOR),
1075 at the stem base or at X-level (N m^{-2}).
1076 τ_T : ontogenetic trend of a dissociated trait T .
1077

1078 **Supplementary material**

1079 Supplementary file: SBcalculation.xls (in .xls format, Microsoft®). This tool makes it possible
1080 to recalculate the safety factors SB of Fig. 3. It can be applied for further assessments of SB,
1081 avoiding the use of two simple formulas (trees of constant diameter, cylindrical, with no
1082 crown and water load, no taper, etc.).

1083

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References

- Achim A, Ruel JC, Gardiner BA, Laflamme G, Meunier S.** 2005. Modelling the vulnerability of balsam fir forests to wind damage. *Forest Ecology and Management* **204**, 35-50.
- Almeras T, Costes E, Salles JC.** 2004. Identification of biomechanical factors involved in stem shape variability between apricot-tree varieties. *Annals of Botany* **93**, 1-14.
- Almeras T, Derycke M, Jaouen G, Beauchene J, Fournier M.** 2009. Functional diversity in gravitropic reaction among tropical seedlings in relation to ecological and developmental traits. *Journal of Experimental Botany* **60**, 4397-4410.
- Almeras T, Fournier M.** 2009. Biomechanical design and long-term stability of trees: Morphological and wood traits involved in the balance between weight increase and the gravitropic reaction. *Journal of Theoretical Biology* **256**, 370-381.
- Almeras T, Gril J, Costes E.** 2002. Bending of apricot tree branches under the weight of axillary growth : test of a mechanical model with experimental data. *Trees-Structure and function* **16**, 5-15.
- Almeras T, Thibaut A, Gril J.** 2005. Effect of circumferential heterogeneity of wood maturation strain, modulus of elasticity and radial growth on the regulation of stem orientation in trees. *Trees-Structure and function* **19**, 457-467.
- Anten NPR, Schieving F.** 2010. The role of wood mass density and mechanical constraints in the economy of tree architecture. *American Naturalist* **175**, 250-260.
- Archer RR, Wilson BF.** 1973. Mechanics of the compression wood response II. On the location, action, and distribution of compression wood formation. *Plant physiology* **51**, 777-782.
- Auclair D, Nepveu G.** 2012. The CAQ network in France: 15 years of brainstorming and cooperative work to connect forest resources and wood quality through modelling approaches and simulation software. *Annals of Forest Science* **69**, 119-123.
- Baltunis BS, Wu HX, Powell MB.** 2007. Inheritance of density, microfibril angle, and modulus of elasticity in juvenile wood of *Pinus radiata* at two locations in Australia. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **37**, 2164-2174.
- Banin L, Feldpausch TR, Phillips OL, Baker TR, Lloyd J, Affum-Baffoe K, Arets EJMM, Berry NJ, Bradford M, Brien RJW, Davies S, Drescher M, Higuchi N, Hilbert DW, Hladik A, Iida Y, Abu Salim K, Kassim AR, King DA, Lopez-Gonzalez G, Metcalfe D, Nilus R, Peh KSH, Reitsma JM, Sonke B, Taedoumg H, Tan S, White L, Woell H, Lewis SL.** 2012. What controls tropical forest architecture? Testing environmental, structural and floristic drivers. *Global Ecology and Biogeography* **21**, 1179-1190.
- Baskin TI, Jensen OE.** 2013. On the role of stress anisotropy in the growth of stems. *Journal of Experimental Botany*. 64 (15), XXXX-XXXX.
- Bastien R, Bohr T, Moulia B, Douady S.** 2013. Unifying model of shoot gravitropism reveals proprioception as a central feature of posture control in plants. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 755-760.
- Boiffin J.** 2008. Variabilité de traits anatomiques, mécaniques et hydrauliques chez les juvéniles de vingt-deux espèces d'arbres de sous-bois en forêt tropicales humide. Master thesis, Université Henri Poincaré, Nancy, France.

- Boudaoud A.** 2010. An introduction to the mechanics of morphogenesis for plant biologists. *Trends in Plant Science*. 15(6):353-60.
- Burgert I.** 2006. Exploring the micromechanical design of plant cell walls. *American journal of botany* **93**, 1391-1401.
- Burgert I, Frühmann K, Keckes J, Fratzl P, Stanzl-Tschegg S.** 2004. Structure-function relationships of four compression wood types: micromechanical properties at the tissue and fibre. *Trees-Structure and function* **18**, 480-485.
- Butler DW, Gleason SM, Davidson I, Onoda Y, Westoby M.** 2012. Safety and streamlining of woody shoots in wind: an empirical study across 39 species in tropical Australia. *New Phytologist* **193**, 137-149.
- Cao J, Tamura Y, Yoshida A.** 2012. Wind tunnel study on aerodynamic characteristics of shrubby specimens of three tree species. *Urban Forestry & Urban Greening* **11**, 465-476.
- Carlquist S.** 2001. *Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood*. Berlin: Springer.
- Chapman CA, Kaufman L, Chapman LJ.** 1998. Buttress formation and directional stress experienced during critical phases of tree development. *Journal of Tropical Ecology* **14**, 341-349.
- Chapotin SM, Razanameharizaka JH, Holbrook NM.** 2006. Abiomechanical perspective on the role of large stem volume and high water content in baobab trees (*Adansonia* spp.; Bombacaceae). *American Journal of Botany* **93**, 1251-1264.
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE.** 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* **12**, 351-366.
- Chevolot M, Louisanna E, Azri W, Leblanc-Fournier N, Roeckel-Drevet P, Scotti-Saintagne C, Scotti I.** 2011. Isolation of primers for candidate genes for mechano-sensing in five Neotropical tree species. *Tree Genetics & Genomes* **7**, 655-661.
- Clair B, Almeras T, Pilate G, Jullien D, Sugiyama J, Riekel C.** 2011. Maturation stress generation in poplar tension wood studied by synchrotron radiation microdiffraction. *Plant Physiology* **155**, 562-570.
- Clair B, Almeras T, Ruelle J, Fournier M.** 2006. Reaction mechanisms for the shape control in angiosperms tension wood : diversity, efficiency, limits and alternatives *Proceedings of the fifth plant biomechanics conference, August 28th-september 1st, 2006, Stockholm, Sweden*. Stockholm, Suède: STFI-Packforsk AB, 467-472.
- Clair B, Fournier M, Prévost MF, Beauchêne J, Bardet S.** 2003. Biomechanics of buttressed trees : bending strains and stresses. *American journal of botany* **90**, 1349-1356.
- Collet C, Fournier M, Ningre F, Hounzandji API, Constant T.** 2011. Growth and posture control strategies in *Fagus sylvatica* and *Acer pseudoplatanus* saplings in response to canopy disturbance. *Annals of Botany* **107**, 1345-1353.
- Coutand C, Fournier M, Moulia B.** 2007. The gravitropic response of poplar trunks: key roles of prestressed wood regulation and the relative kinetics of cambial growth versus wood maturation. *Plant physiology* **144**, 1166-1180.
- Darwin C, Darwin FE.** 1880. *The Power of movement in plants*. London: Murray.
- Dassot M, Constant T, Fournier M.** 2011. The use of terrestrial LiDAR technology in forest science: application fields, benefits and challenges. *Annals of Forest Science* **68**, 959-974.

- Dassot M, Fournier M, Ningre F, Constant T.** 2012. Effect of tree size and competition on tension wood production over time in beech plantations and assessing relative gravitropic response with a biomechanical model. *American Journal of Botany* **99**, 1427-1435.
- Dean TJ, Long JN.** 1986. Validity of constant stress and elastic-principles of stem formation in *Pinus contorta* and *Trifolium pratense*. *Annals of Botany* **58**, 833-740.
- de Langre E.** 2008. Effects of wind on plants. *Annual Review of Fluid Mechanics* **40**, 141-168.
- Delcamp M, Gourlet-Fleury S, Flores O, Gamier E.** 2008. Can functional classification of tropical trees predict population dynamics after disturbance? *Journal of Vegetation Science* **19**, 209-220.
- Donaldson L.** 2008. Microfibril angle: measurement, variation and relationship - a review. *IAWA Bulletin* **29**, 345-386.
- Duchateau E.** 2008. Diversité des capacités de réaction gravitropique de jeunes arbres en forêt tropicale humide. Master thesis, Université Henri Poincaré, Nancy, France.
- Eloy C.** 2011. Leonardo's rule, self-similarity, and wind-induced stresses in trees. *Physical Review Letters* **107**.
- Ennos AR.** 2000. The mechanics of root anchorage. *Advances in Botanical Research Incorporating Advances in Plant Pathology* **33**, 133-157.
- Evans R, Ilic J.** 2001. Rapid prediction of wood stiffness from microfibril angle and density. *Forest products journal* **51**, 53 - 57.
- Fengel D, Wegener G.** 1984. *Wood. Chemistry, ultrastructure, reactions*. Berlin/New York: de Gruyter.
- Ferrand JC.** 1982. Study of growth stresses:1. Measurement method on increment cores. *Annales Des Sciences Forestieres* **39**, 109-142.
- Fortunel C, Fine PVA, Baraloto C.** 2012. Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Functional Ecology* **26**, 1153-1161.
- Fournier M, Baillères H, Chanson B.** 1994a. Tree biomechanics : growth, cumulative prestresses, and reorientations. *Biomimetics* **2**, 229-251.
- Fournier M, Chanson B, Thibaut B, Guitard D.** 1994b. Measurement of residual growth strains at the stem surface. Observations on different species. *Annales Des Sciences Forestieres* **51**, 249-266.
- Fournier M, Stokes A, Coutand C, Fourcaud T, Moulia B.** 2006. Tree biomechanics and growth strategies in the context of forest functional ecology . In: Herrel A, Speck T, Rowe N, eds. *Ecology and biomechanics: a mechanical approach to the ecology of animals and plants*. Boca Raton, Florida, USA: CRC Press, 1-34.
- Gardiner B, Byrne K, Hale S, Kamimura K, Mitchell SJ, Peltola H, Ruel J-C.** 2008. A review of mechanistic modelling of wind damage risk to forests. *Forestry* **81**, 447-463.
- Gibson LJ, Ashby MF.** 1997. *Cellular solids. Structure and properties*. Cambridge: Cambridge University Press.
- Givnish TJ.** 2002. Ecological constraints on the evolution of plasticity in plants. *Evolutionary Ecology* **16**, 213-242.
- Gordon JE.** 1978. *Structures or why things do not fall down*. Harmondsworth, Penquin Books Ltd.

- Greenhill A.** 1881. Determination of the greatest height consistent with stability that a vertical pole or mast can be made, and of the greatest height to which a tree of given proportions can grow. *Proceedings of the Cambridge Philosophical Society*, Vol. 4, 65-73.
- Grime JP.** 2001. *Plant strategies, vegetation processes, and ecosystem properties*. Chichester; UK: John Wiley & Sons Ltd.
- Hamilton JR, Thomas CK, Carvell KL.** 1985. Tension wood formation following release of upland oak advance reproduction. *Wood and fiber science* **17**, 382-390.
- Hejnowicz Z.** 1997. Graviresponses in herbs and trees: A major role for the redistribution of tissue and growth stresses. *Planta* **203**, S136-S146.
- Herault B, Bachelot B, Poorter L, Rossi V, Bongers F, Chave J, Paine CET, Wagner F, Baraloto C.** 2011. Functional traits shape ontogenetic growth trajectories of rain forest tree species. *Journal of Ecology* **99**, 1431-1440.
- Holbrook NM, Putz FE.** 1989. Influence of neighbors on tree form : effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (sweet gum). *American journal of botany* **76**, 1740-1749.
- Huang YS, Hung LF, Kuo-Huang LL.** 2010. Biomechanical modeling of gravitropic response of branches: roles of asymmetric periphery growth strain versus self-weight bending effect. *Trees-Structure and Function* **24**, 1151-1161.
- Iino M.** 2006. Toward understanding the ecological functions of tropisms: interactions among and effects of light on tropisms. *Current Opinion in Plant Biology* **9**, 89-93.
- James KR, Haritos N, Ades PK.** 2006. Mechanical stability of trees under dynamic loads. *American journal of Botany* **93**, 1522-1530.
- Jaouen G.** 2007. Etude des stratégies biomécaniques de croissance des jeunes arbres en peuplement hétérogène tropical humide. *Thèse de doctorat, Université Henri Poincaré, Nancy, France*. 201p.
- Jaouen G, Almeras T, Coutand C, Fournier M.** 2007. How to determine sapling buckling risk with only a few measurements. *American Journal of Botany* **94**, 1583-1593.
- Jaouen G, Fournier M, Almeras T.** 2010. Thigmomorphogenesis versus light in biomechanical growth strategies of saplings of two tropical rain forest tree species. *Annals of Forest Science* **67**, 211.
- Johnson EA, Miyanishi K.** 2007. *Plant disturbance ecology: the process and the response*. Academic Press.
- Jullien D, Widmann R, Loup C, Thibaut B.** 2013. Relationship between tree morphology and growth stress in mature European beech stands. *Annals of Forest Science* **70**, 133-142.
- Jungnickl K, Goebbels J, Burgert I, Fratzl P.** 2009. The role of material properties for the mechanical adaptation at branch junctions. *Trees-Structure and Function* **23**, 605-610.
- Kellogg RM, Wangaard FF.** 1969. Variation in the cell-wall density of wood. *Wood and Fiber Science* **1**, 180-204.
- King D, Loucks OL.** 1978. Theory of tree bole and branch form. *Radiation and Environmental Biophysics* **15**, 141-165.
- King DA, Davies SJ, Tan S, Noor NSM.** 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology* **94**, 670-680.
- King DA, Davies SJ, Tan S, Noor NSM.** 2009. Trees approach gravitational limits to height in tall lowland forests of Malaysia. *Functional Ecology* **23**, 284-291.

- Kooyman RM, Westoby M.** 2009. Costs of height gain in rainforest saplings: main-stem scaling, functional traits and strategy variation across 75 species. *Annals of Botany* **104**, 987-993.
- Lachenbruch B, Johnson GR, Downes GM, Evans R.** 2010. Relationships of density, microfibril angle, and sound velocity with stiffness and strength in mature wood of Douglas-fir. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* **40**, 55-64.
- Lachenbruch B, Moore JR, Evans R.** 2011. Radial variation in wood structure and function in woody plants, and hypotheses for its occurrence. In: Meinzer FC, Lachenbruch B, Dawson TE, eds. *Size-and age-related changes in tree structure and function*. Netherlands: Springer, 121-164.
- Lang AC, Haerdtle W, Bruelheide H, Geissler C, Nadrowski K, Schuldt A, Yu M, von Oheimb G.** 2010. Tree morphology responds to neighbourhood competition and slope in species-rich forests of subtropical China. *Forest Ecology and Management* **260**, 1708-1715.
- Larjavaara M.** 2010. Maintenance cost, toppling risk and size of trees in a self-thinning stand. *Journal of Theoretical Biology* **265**, 63-67.
- Larjavaara M, Muller-Landau HC.** 2010. Rethinking the value of high wood density. *Functional Ecology* **24**, 701-705.
- Larjavaara M, Muller-Landau HC.** 2012. Still rethinking the value of high wood density. *American Journal of Botany* **99**, 165-168.
- Lens F, Smets E, Melzer S.** 2012. Stem anatomy supports *Arabidopsis thaliana* as a model for insular woodiness. *New Phytologist* **193**, 12-17.
- Lopez D, Michelin S, de Langre E.** 2011. Flow-induced pruning of branched systems and brittle reconfiguration. *Journal of Theoretical Biology* **284**, 117-124.
- McMahon, TA.** 1973. Size and shape in biology. *Science* **179**, 1202-1204.
- Makela A, Grace JC, Deckmyn G, Kantola A, Campioli M.** 2010. Simulating wood quality in forest management models. *Forest Systems* **19**, 48-68.
- Martínez-Cabrera HI, Schenk HJ, Cevallos-Ferriz SRS, Jones CS.** 2011. Integration of vessel traits, wood density, and height in angiosperm shrubs and trees. *American Journal of Botany* **98**, 915-922.
- Martone PT, Boller M, Burgert I, Dumais J, Edwards J, Mach K, Rowe N, Rüggeberg M, Seidel R, Speck T.** 2010. Mechanics without muscle: Biomechanical inspiration from the plant world. *Integrative and Comparative Biology* **50**, 888-907.
- Matsuzaki J, Masumori M, Tange T.** 2006. Stem phototropism of trees: A possible significant factor in determining stem inclination on forest slopes. *Annals of Botany* **98**, 573-581.
- Medhurst J, Downes G, Ottenschlaeger M, Harwood C, Evans R, Beadle C.** 2012. Intra-specific competition and the radial development of wood density, microfibril angle and modulus of elasticity in plantation-grown *Eucalyptus nitens*. *Trees-Structure and Function* **26**, 1771-1780.
- Menard L, McKey D, Rowe, N. (2009)** Developmental plasticity and biomechanics of treelets and lianas in *Manihot aff. quinquepartita* (Euphorbiaceae): a branch-angle climber of French Guiana. *Annals of Botany* **103**, 1249-1259.

- Moulia B.** 2013. Plant biomechanics and mechanobiology are convergent paths to flourishing interdisciplinary research. *Journal of Experimental Botany* 64 (15), XXXX-XXXX.
- Moulia B, Coutand C, Lenne C.** 2006. Posture control and skeletal mechanical acclimation in terrestrial plants: implications for mechanical modeling of plant architecture. *American Journal of Botany* **93**, 1477-1489.
- Moulia B, Fournier-Djimbi M.** 1997. Optimal mechanical design of plant stems: the models behind the allometric power laws. In: *Proceedings of the First Plant Biomechanics Conference*. Reading, Centre for Biomimetics, Vincent JFV and Jeronimidis G (Eds).
- Moulia B, Fournier M.** 2009. The power and control of gravitropic movements in plants: a biomechanical and systems biology view. *Journal of Experimental Botany* **60**, 461-486.
- Moulia B, Der Loughian C, Bastien R, Martin O, Rodríguez M, Gourcilleau D, Barbacci A, Badel E, Franchel G, Lenne C, Roeckel-Drevet P, Allain JM, Frachisse JM, Langre E, Coutand C, Fournier-Leblanc N, Julien JL.** 2011. Integrative mechanobiology of growth and architectural development in changing mechanical environments. In: Wojtaszek P, ed. *Mechanical Integration of Plant Cells and Plants*, Springer Berlin Heidelberg. **9**, 269-302.
- Niklas KJ.** 1988. Dependency of the tensile modulus on transverse dimensions, water potential, and cell number of pith parenchyma. *American Journal of Botany* **75**, 1286-1292.
- Niklas KJ.** 1992. *Plant biomechanics An engineering approach to plant form and function*. Chicago: University of Chicago Press.
- Niklas KJ.** 1994. *Plant allometry. The scaling of form and process*. Chicago: University of Chicago Press.
- Niklas KJ.** 1997. Mechanical properties of Black Locust (*Robinia pseudoacacia* L.) wood. Size- and age-dependent variations in sap- and heartwood. *Annals of botany* **79**, 265-272.
- Niklas KJ.** 2000. Computing factors of safety against wind-induced tree stem damage. *Journal of Experimental Botany* **51**, 797-806.
- Niklas KJ.** 2007. Maximum plant height and the biophysical factors that limit it. *Tree Physiology* **27**, 433-440.
- Niklas KJ, Cobb ED, Marler T.** 2006a. A comparison between the record height-to-stem diameter allometries of pachycaulis and leptocaulis species. *Annals of Botany* **97**, 79-83.
- Niklas KJ, Spatz H-C.** 2000. Response to Klaus Mattheck's letter. *Trees-Structure and Function* **15**, 64-65.
- Niklas KJ, Spatz HC.** 2004. Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 15661-15663.
- Niklas KJ, Spatz HC.** 2010. Worldwide correlations of mechanical properties and green wood density. *American Journal of Botany* **97**, 1587-1594.
- Niklas KJ, Spatz HC, Vincent J.** 2006b. Plant biomechanics: an overview and prospectus. *American journal of botany* **93**, 1369-1378.
- Osunkoya OO, Omar-Ali K, Amit N, Dayan J, Daud DS, Sheng TK.** 2007. Comparative height-crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. *American Journal of Botany* **94**, 1951-1962.
- Plucinski M, Plucinski S, Rodriguez-Iturbe I.** 2008. Consequences of the fractal architecture of trees on their structural measures. *Journal of Theoretical Biology* **251**, 82-92.

- Read J, Evans R, Sanson GD, Kerr S, Jaffre T.** 2011. Wood properties and trunk allometry of co-occurring rainforest canopy trees in a cyclone-prone environment. *American Journal of Botany* **98**, 1762-1772.
- Read J, Stokes A.** 2006. Plant biomechanics in an ecological context. *American Journal of Botany* **93**, 1546-1565.
- Rodriguez M, Langre Ed, Moulia B.** 2008. A scaling law for the effects of architecture and allometry on tree vibration modes suggests a biological tuning to modal compartmentalization. *American Journal of Botany* **95**, 1523-1537.
- Rowe N, Speck T.** 2005. Plant growth forms: an ecological and evolutionary perspective. *New phytologist* **166**, 61-72.
- Salmen L, Burgert I.** 2009. Cell wall features with regard to mechanical performance. A review COST Action E35 2004-2008: Wood machining - micromechanics and fracture. *Holzforschung* **63**, 121-129.
- Saren MP, Serimaa R, Andersson S, Saranpaa P, Keckes J, Fratzl P.** 2004. Effect of growth rate on mean microfibril angle and cross-sectional shape of tracheids of Norway spruce. *Trees-Structure and Function* **18**, 354-362.
- Schindler D, Bauhus J, Mayer H.** 2012. Wind effects on trees. *European Journal of Forest Research* **131**, 159-163.
- Scurfield G.** 1973. Reaction wood: Its structure and function. *Science* **179**, 647-655.
- Sellier D, Fourcaud T.** 2009. Crown structure and wood properties: Influence on tree sway and response to high winds. *American Journal of Botany* **96**, 885-896.
- Siau JF.** 1984. Transport processes in wood. Berlin Heidelberg: Springer.
- Sierra-De-Grado R, Pando V, Martinez-Zurimendi P, Penalvo A, Bascones E, Moulia B.** 2008. Biomechanical differences in the stem straightening process among *Pinus pinaster* provenances. A new approach for early selection of stem straightness. *Tree Physiology* **28**, 835-846.
- Sterck FJ, Bongers F.** 1998. Ontogenetic changes in size, allometry, and mechanical design of tropical rain forest trees. *American Journal of Botany* **85**, 266-272.
- Stokes A.** 2000. *The supporting roots of trees and woody plants: form, function and physiology*. Dordrecht, Netherlands: Kluwer Academic Publishers.
- Swenson NG, Enquist BJ.** 2007. Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* **94**, 451-459.
- Taneda H, Tateno M.** 2004. The criteria for biomass partitioning of the current shoot: Water transport versus mechanical support. *American Journal of Botany* **91**, 1949-1959.
- Tateno M.** 1991. Increase in lodging safety factor on thigmomorphogenetically dwarfed shoots of mulberry tree. *Physiologia Plantarum* **81**, 239-243.
- Tobin B, Cermak J, Chiatante D, Danjon F, Di Iorio A, Dupuy L, Eshel A, Jourdan C, Kallioikoski T, Laiho R, Nadezhdina N, Nicoll B, Pages L, Silva J, Spanos I.** 2007. Towards developmental modelling of tree root systems. *Plant Biosystems* **141**, 481-501.
- Turner IM.** 2001. *The ecology of trees in the tropical rain forest*. Cambridge: Cambridge University Press.
- van Gelder HA, Poorter L, Sterck FJ.** 2006. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. *New Phytologist* **171**, 367-378.

- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E.** 2007. Let the concept of trait be functional! *Oikos* **116**, 882-892.
- Waghorn MJ, Watt MS.** 2013. Stand variation in *Pinus radiata* and its relationship with allometric scaling and critical buckling height. *Annals of Botany* **111**, 675-680.
- Watt MS, Moore JR, Facon J-P, Downes GM, Clinton PW, Coker G, Davis MR, Simcock R, Parfitt RL, Dando J, Mason EG, Bown HE.** 2006. Modelling environmental variation in Young's modulus for *Pinus radiata* and implications for determination of critical buckling height. *Annals of Botany* **98**, 765-775.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ.** 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**, 125-159.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R.** 2004. The worldwide leaf economics spectrum. *Nature* **428**, 821-827.
- Wright SD, McConnaughay KDM.** 2012. Interpreting phenotypic plasticity: the importance of ontogeny. *Plant Species Biology* **17**: 119-131.
- Sultan SE.** 2000. Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science* **5**, 537-542.
- Xu P, Liu H.** 2004. Models of microfibril elastic modulus parallel to the cell axis. *Wood Science and Technology* **38**, 363-374.
- Yang JL, Bailleres H, Evans R, Downes G.** 2006. Evaluating growth strain of *Eucalyptus globulus* Labill. from SilviScan measurements. *Holzforschung* **60**, 574-579.
- Yang JL, Evans R.** 2003. Prediction of MOE of eucalypt wood from microfibril angle and density. *Holz als Roh und Werkstoff* **61**, 449-452.
- Yoshida M, Okuyama T.** 2002. Techniques for measuring growth stress on the xylem surface using strain and dial gauges. *Holzforschung* **56**, 461-467.
- Zhang S-B, Slik JWF, Zhang J-L, Cao K-F.** 2011. Spatial patterns of wood traits in China are controlled by phylogeny and the environment. *Global Ecology and Biogeography* **20**, 241-250.

Legends of tables

Table 1: Synthesis of the four traits: Safety against Wind (SW) as the critical wind pressure, Safety against Self-Buckling (SB) as the ratio of critical buckling height for the same trunk volume, to current height, Motricity (MV) as the active gravitropic curvature rate during radial growth, Posture Control performance (PC) as the ratio of the gravitropic curvature to the gravitational one, at a given angle ϕ (the limit 1 is the long-term stable regime where the tree maintains a constant lean ϕ). For each trait, the table summarizes the way to calculate it as a combination of dissociated variables, the types of the different variables involved (size, shape, wood, load), and the allometric scaling laws between size variables that maintain a constant value.

Table 2: General method for assessing ontogenetic trends on an integrative trait from a sampling of trees that represent an ontogenetic trajectory (case study: safety against self-buckling of a sample of *Oxandra asbeckii* at the sapling stage, re-analysing data from Jaouen *et al.* (2007)). The first two lines provide the mean values and the coefficient of variation for each component T. The third line τ_T is the power exponent (ontogenetic trend) from fitting the trait T to the developmental variable H. The fourth v_T gives the power of T in the integrative trait SB. In the last line, the sum of products $\tau_T v_T$ gives the ontogenetic trend of the integrative trait (SB in this case), broken down into trends for each component.

Table 3: Scaling of E with ρ and $\cos^4(\text{MFA})$ using data from Read *et al.* (2011) and Boiffin (2008). Wood characteristics were measured on increment cores and silviscan (X-ray tomography and diffraction) in Read *et al.* (2011), whereas Boiffin (2008) measured E of entire stems in a universal testing machine (bending test), and MFA by X-ray diffraction.

Table 1 (erratum : ligne 2 trait SB remplacer 2+1 par 2n+1)

Trait	Expression as a function of size, wood, load and shape variables	Size variables	Resulting scaling laws between size variables to maintain a stable trait (everything else being constant)	Shape factors	Wood resistance or motor properties	Load factors
SW	$\frac{\pi \sigma_c D^3}{16 c_d A_w H k_w F_w}$	D, A_w, H	$D^3 \sim A_w H$	k_w, F_w	σ_c	c_d, k_w, F_w, A_w
SB	$0.88 H^{-1} V^{1/4} E^{1/4} (\rho_T g)^{-1/4} F_b^{1/2}$ or $0.83 H^{-3/4} D^{1/2} E^{1/4} (\rho_T g)^{-1/4} (2+1)^{-1/4} F_b^{1/2}$	$H, V \text{ or } D$	$H \sim V^{1/4}$ or $H \sim D^{2/3}$	F_b	E	ρ_T
MV	$-4 \frac{F_m \Delta \alpha}{D^2} \frac{dD}{dt}$	$\frac{dD}{dt}, D$	$\frac{dD}{dt} \sim D^2$	-	$\Delta \alpha$	-
PC	$\frac{E \Delta \alpha}{4(1+b) \rho_T g \sin \varphi} \frac{F_m D}{F_g H^2}$	H, D	$H \sim D^{1/2}$	b, F_g	$E, \Delta \alpha$	$\rho_T, \sin \varphi$

Table 2

Trait T	H (m)	V (m ³)	ρ_T (g/cm ³)	F_b	E (MPa)	SB
Mean value	7.0	7.5 10 ⁻³	1.6	2.2	14200	1.41
Coefficient of variation (%)	40%	155%	22%	18%	10%	18%
Ontogenetic trends, τ_T ($T \approx H^{\tau_T}$)	1	2.726	-0.097	0.128	-0.018	-0.235
Power of T in SB formula, v_T	-1	0.25	-0.25	0.5	0.25	-
$v_T \tau_T$: Contribution of T to SB	-1	0.68	0.024	0.065	-0.005	-0.235

Table 3

Wood trait T	ρ	$\cos^4(\text{MFA})$	E
Mean value			
Boiffin	0.64	MFA=15°	12.2 GPa
Read	0.66	MFA=12°	14.3 GPa
Pearson coefficient of LogE vs. LogT			
Boiffin	0.78	0.25	1
Read	0.79	0.83	1
Pearson coefficient of Logp vs. LogT			
Boiffin	1	0.08	0.78
Read	1	0.75	0.79

Legends of figures

Figure 1: The four different processes of biomechanical traits with graphical representations of geometrical traits.

Figure 2: Reproduced from Niklas (2000). Safety against wind inside one wild cherry tree as a function of distance from top of tree (H-X). The safety factor here is the dimensionless quotient of the critical wind pressure to the wind drag pressure experienced at the stem element level (83 segments of the same tree were used in the numerical computation). The tree safety is then characterised by a set of safety factors along the the tree height X. Three different wind speeds (10, 20 and 50 m/s) are simulated, leading to three different safety factors for the same stem element design. The single safety factor SW defined in the text can be calculated from the minimum values of Niklas's safety factor along the height, at different wind speeds, as $\rho_{air} U_w^2 \min(U_w)$. On the right side, tree silhouette and measured wind speed profiles.

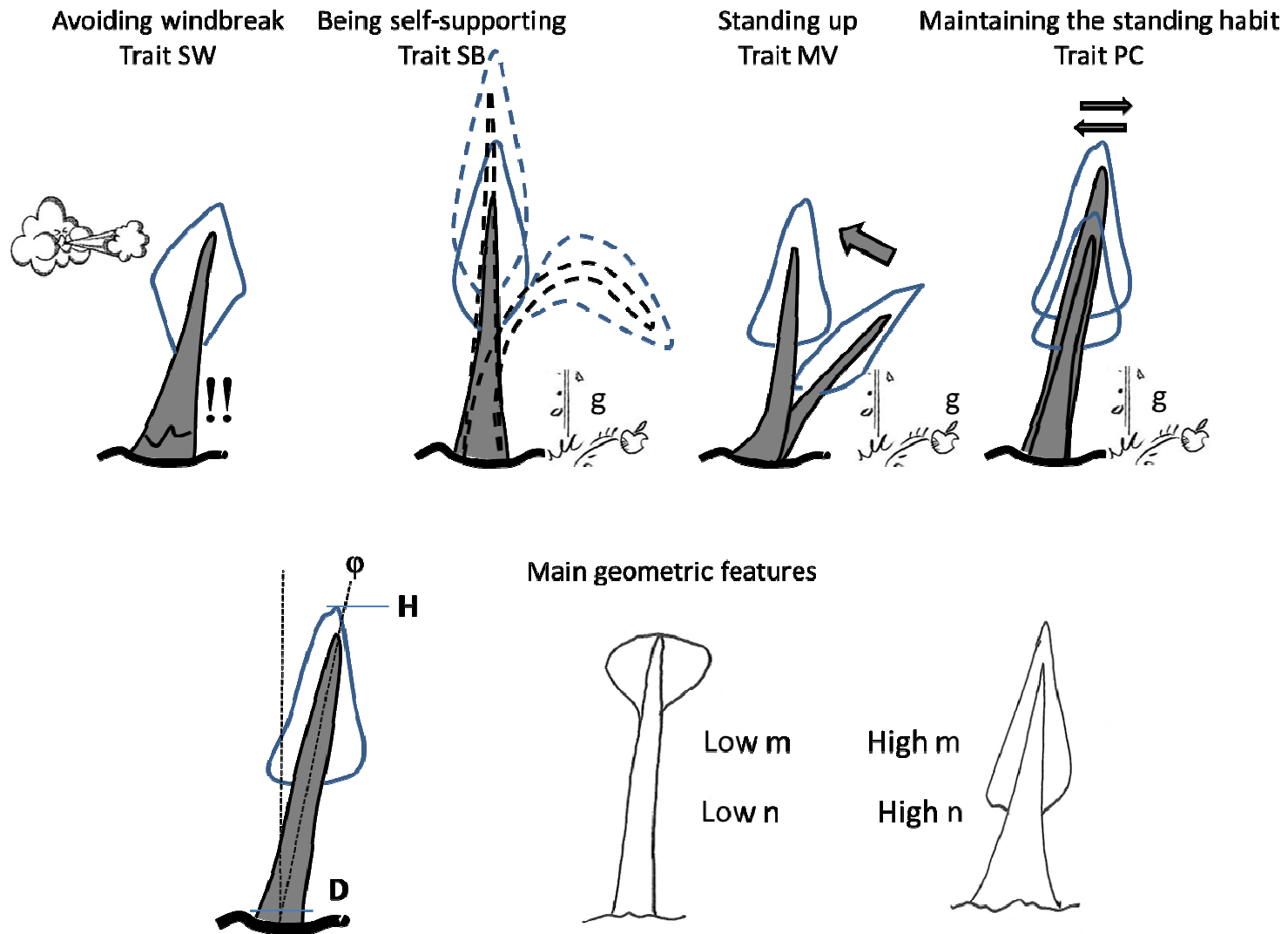
Figure 3: Variations of safety factors against self-buckling SB as a function of wood basic density ρ , independently of size and slenderness. SB was calculated for a tree of constant $D=20$ cm and $H=20$ m: **(i)** Cylinder made of dry wood: safety factor calculated from the maximum height at a constant diameter (as done in Sterck and Bongers, 1998); **(ii)** Cylinder made of fresh wood: safety factor calculated from the maximum height at a constant wood volume; **(iii)** Tapered stem: everything else similar to (ii); **(iv)** Crowned stem, which is the (iii) situation with additional loads of branches; and **(v)** Crowned tree carrying epiphytes, i.e., (iv) where a quite small mass but with a high centre of mass has been added. Wood modulus of elasticity E is linked to wood basic density (equation 3). The density ρ_T is given by ρ in **(i)**, wood fresh density given by equation (2) in **(ii)** and **(iii)**, a mean value of 1400 kg/m^3 in **(iv)** (mean value of Jaouen *et al.*, 2007), a mean value of 1540 kg/m^3 in **(v)** assuming the biomass of epiphytes is 10% of the tree biomass. Except for cylinders (i) and (ii) where $n=0$, the taper n is 0.6 (mean value observed by Jaouen *et al.*, 2007). The biomass profile distribution is $m=2n+1$ for the tapered stem **(iii)**, $m=1.5$ (mean value observed by Jaouen *et al.*, 2007) for the crowned stem **(iv)**, and $m=1.27$ in **(v)**, which means that the centre of mass of epiphytes is located at 80% of the total tree height. SB is constant with ρ in (i), scales as $\rho^{0.22}$ in (ii) and (iii), and as $\rho^{0.26}$ in (iv) and (v).

Figure 4: Relationships between mortality rate and biomechanical traits PC and SB at sapling stages on a set of tropical species. Spearman correlation coefficients are $R=-0.55$ ($p=0.07$) for PC and $R=-0.47$ ($p=0.14$) for SB. Observations from the experimental plots of Paracou in French Guiana (Jaouen *et al.*, 2007; Delcamp *et al.*, 2008). Mortality rates are those of Delcamp *et al.* (2008) for control (not harvested) plots. Functional groups are also developed in Delcamp *et al.* (2008): ST = strongly shade-tolerant species, small to medium size; T = shade-tolerant species, medium size; MT = mid shade-tolerant species,

emergent; H = long-lived heliophilous species of the canopy. The species biomechanical traits were calculated as in Jaouen *et al.* (2007), on 1370 saplings for morphological data (H, D, b and ϕ) and sub-sampling for other variables (m, n, ρ_T , E, $\Delta\alpha$). All data comes from Jaouen (2007) except $\Delta\alpha$ in PC. $\Delta\alpha$ data come from the Wood Diversity project (Duchateau, 2008). Since Duchateau (2008) presented results on only nine species, unpublished data on *Eperua falcata* and *Pradosia cochlearia* has been added.

Figure 5: Basal (between 0 and 2 m) leans on a community of tropical saplings. Plain lines represent leans simulated under the assumption of no motricity (PC=0), along growth trajectories, from an initial disturbance of 8 degrees at an initial diameter (at 1 m in height) of 1 cm. Simulations used the equation of the gravitational curvature rate $\frac{dC_g}{dD}$ and mean traits measured on each species, as developed in Jaouen (2007). Dots are observed leans for the whole set of trees and species (adapted from Jaouen, 2007).

Figure 1



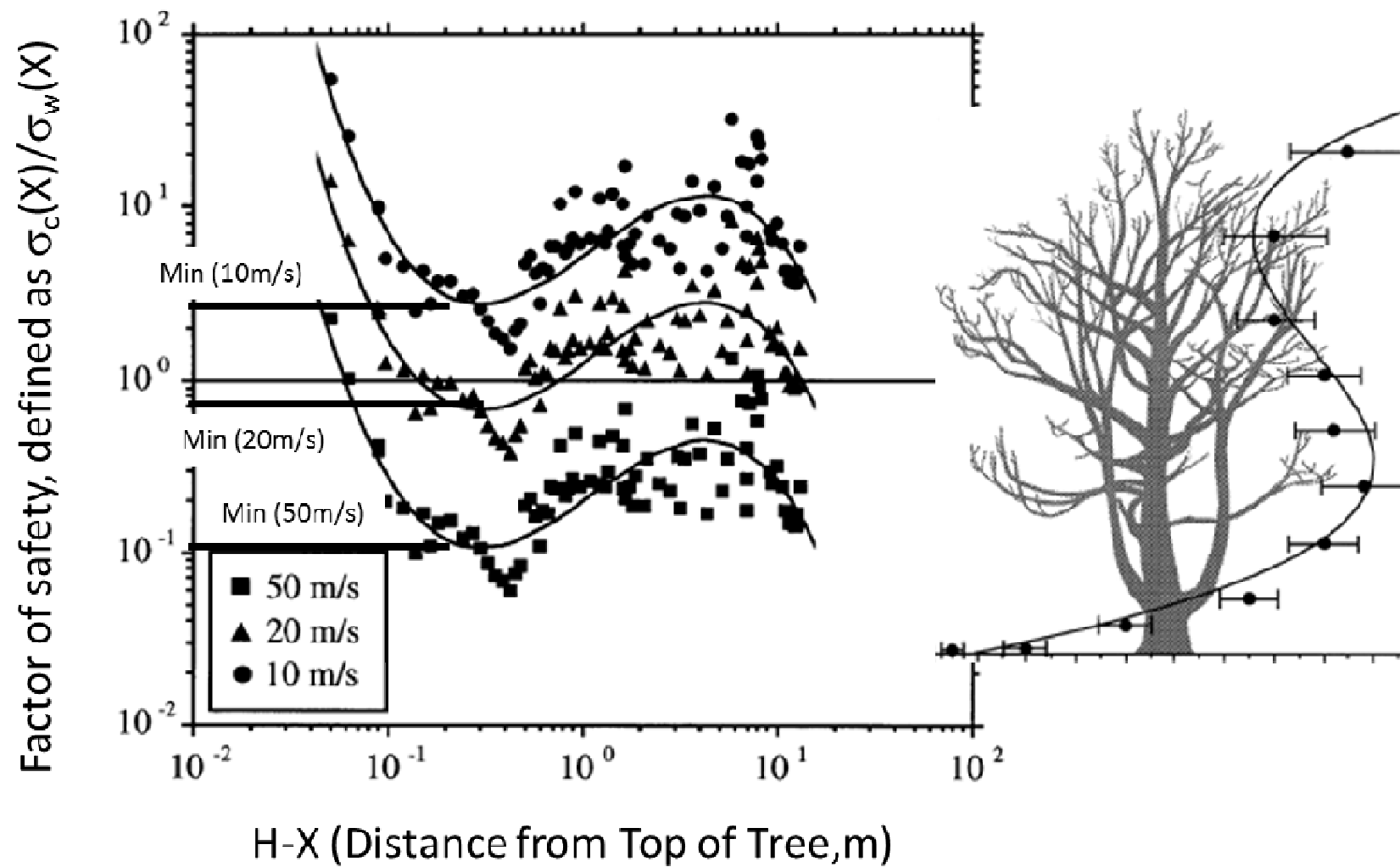


Figure3

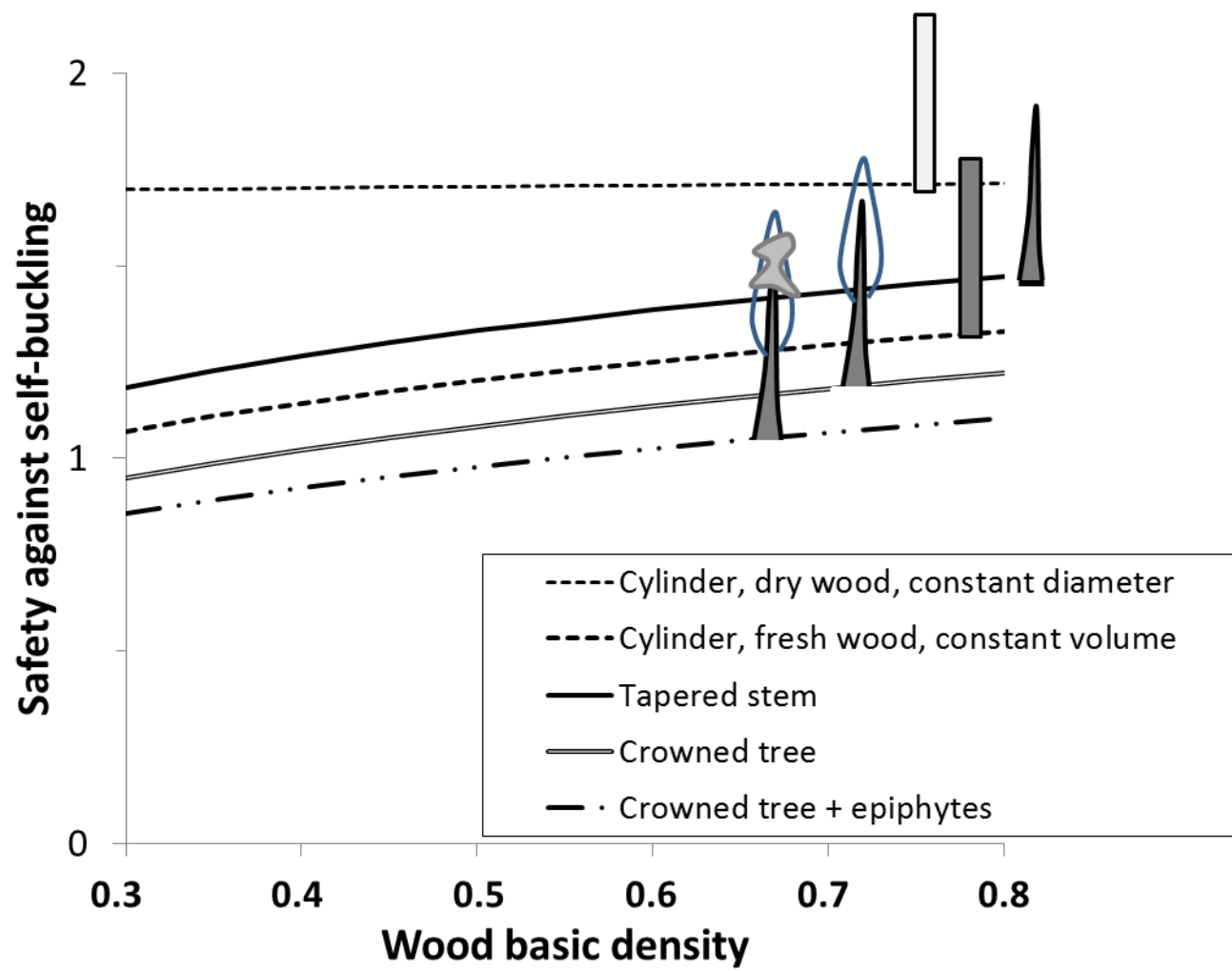


Figure 4

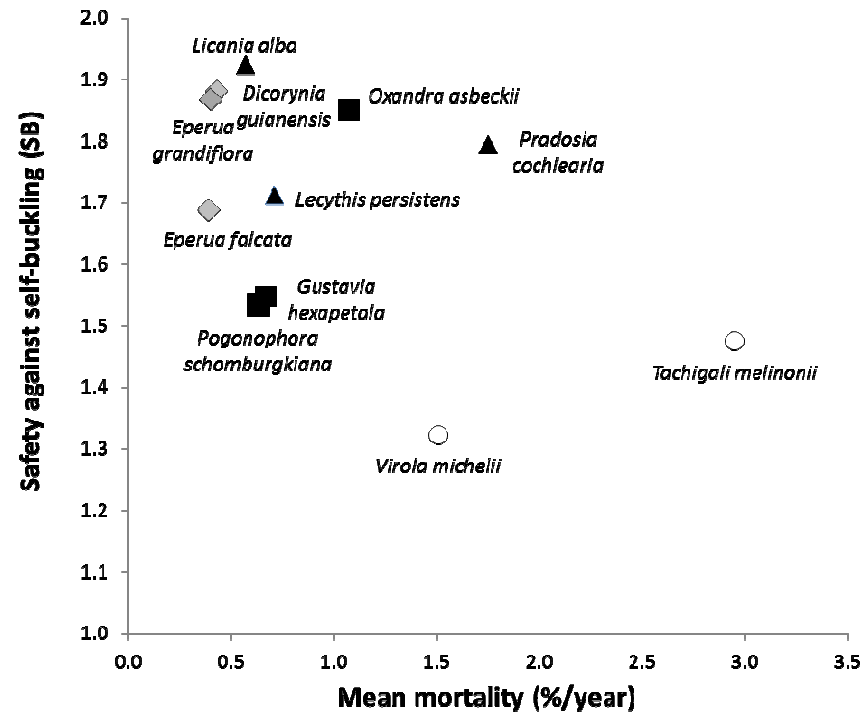
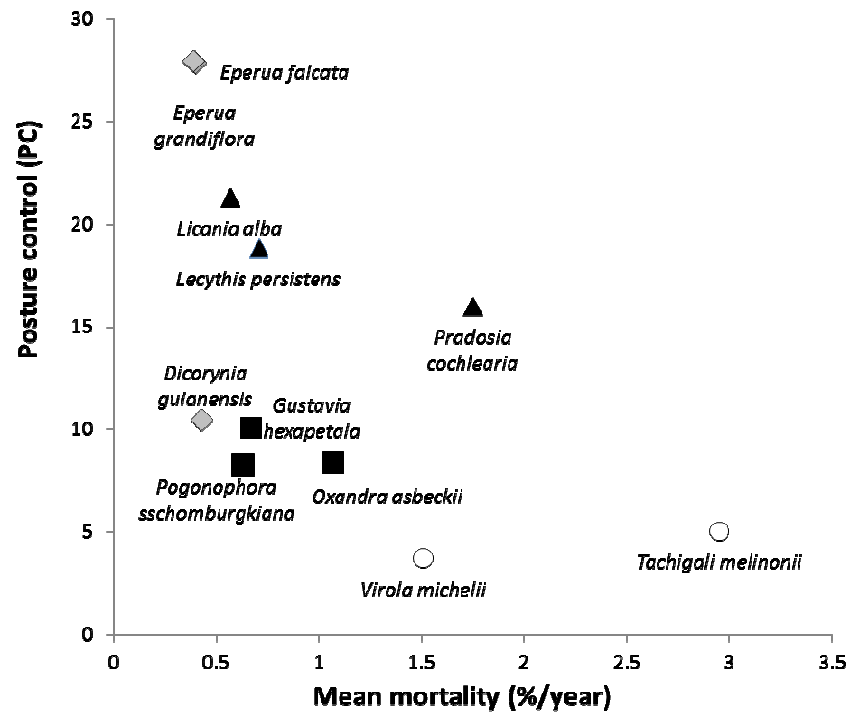


Figure 5

